THE FEEDING BIOMECHANICS OF JUVENILE RED SNAPPER (*LUTJANUS CAMPECHANUS*) FROM THE NORTHWESTERN GULF OF MEXICO

A Thesis

by

JANELLE ELAINE CASE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2007

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Christopher D. Marshall
Committee Members,	Jay R. Rooker
	Thomas DeWitt
Head of Department,	Delbert Gatlin

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ABSTRACT

The Feeding Biomechanics of Juvenile Red Snapper (*Lutjanus campechanus*) from the Northwestern Gulf of Mexico. (May 2007)

Janelle Elaine Case, B.S., Texas A&M University at Galveston

Chair of Advisory Committee: Dr. Christopher D. Marshall

Juvenile red snapper are attracted to structure and settle onto low profile reefs, which serve as nursery grounds. Little is known about their life history during this time. However, recent studies from a shell bank in the NW Gulf of Mexico have shown higher growth rates for juveniles located on mud habitats adjacent to low profile reefs, perhaps due to varied prey availability and abundance. To further investigate the habitat needs of juvenile red snapper, individuals were collected from a low profile shell ridge (on-ridge) and adjacent mud areas (off-ridge) on Freeport Rocks, TX, and divided into three size classes (≤3.9 cm SL, 4.0-5.9 cm SL, ≥6 cm SL). Feeding morphology and kinematics were characterized and compared among size classes and between the two habitats. A dynamic jaw lever model was used to make predictions about feeding mechanics, and kinematic profiles obtained from high-speed videos of prey capture events validated the model's predictive ability. Model output suggested an ontogenetic shift in feeding morphology from a juvenile feeding mode (more suction) to an adult feeding mode (more biting). Stomach contents revealed a concomitant shift in prey composition that coincided with the ontogenetic shift in feeding mode. The model also predicted that on-ridge

juveniles would have faster jaw closing velocities compared to off-ridge juveniles, which had slower, stronger jaws. Analysis of prey capture events indicated that on-ridge juveniles demonstrated greater velocities and larger displacements of the jaws than off-ridge juveniles. Shape analysis was used to further investigate habitat effects on morphology. Off-ridge juveniles differed from on-ridge in possessing a deeper head and body. Results from model simulations, kinematic profiles, personal observations, and shape analysis all complement the conclusion that on-ridge juveniles exhibited more suction feeding behavior, whereas off-ridge juveniles used more biting behavior. Stomach contents demonstrated an early switch to piscivory in off-ridge juveniles compared to on-ridge juveniles, which may account for higher off-ridge growth rates. Habitat disparity, perhaps available prey composition, generated variations in juvenile feeding mechanics and consequently feeding behavior. This disparity may ultimately affect the growth rates and recruitment success of juvenile red snapper from different habitats.

DEDICATION

To my grandparents

ACKNOWLEDGMENTS

I wish to express my deepest appreciation to my advisor, Christopher Marshall, for his continual guidance, support, and friendship. He has proven himself to be an excellent role model, not only academically, but also as a person. Thank you. I also thank my other committee members, Drs. Thomas DeWitt and Jay Rooker, for their bountiful amount of knowledge. In addition, I would like to thank my family, from whom I received an unlimited amount of encouragement. I give countless thanks to Joe Mikulas and Ryan Schloesser for their tireless help in collecting fish and in keeping them alive. Lastly, this project would not have been possible without the generous support of the Texas A&M at Galveston Marine Biology Department, NOAA's Marine Fisheries Initiative Program (MARFIN) (grant # NA17FF2872 to Jay R. Rooker), and donations from the Luke and Erma Lee Mooney Student Travel Grant.

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INTRODUCTION

Red Snapper

The red snapper (*Lutjanus campechanus*) fishery is the second most important commercial fishery in the Gulf of Mexico after shrimping. Red snapper landings have been on a continuous decline and are now one of the most overexploited species in the Gulf of Mexico (Baker *et al.* 1998 and GMFMC 2000). In addition to adult red snapper being overfished, the bycatch associated with the shrimping industry removes a substantial portion of the young juveniles (Goodyear 1994, Waters 1996, Schirripa and Legault 1997). This has a significant negative impact on the fishery because early life mortality affects recruitment and year-class strength. Recent efforts have focused on the identification of favorable habitat for early life development of juvenile red snapper, because such identification is essential in developing proper and effective management plans.

Larval red snapper settle out of the water column at approximately 16 mm (Rooker *et al*. 2004) and are attracted to complex habitats, such as low profile reefs and shell habitats, which serve as essential nursery grounds for juveniles (Szedlmayer and Howe 1997). The settlement patterns within these habitats remain unclear. Significant higher recruitment was reported on shell ridges (on-ridge) in the northeastern Gulf of Mexico (Szedlmayer and Conti 1999) and on

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adjacent mud habitats (off-ridge) in the northwestern Gulf of Mexico (Rooker *et al*. 2004). This suggests that factors other than structure, perhaps prey availability, may influence settlement patterns.

Spatial variation in structure can affect the composition and availability of prey items; therefore, available prey resources may differ between off-ridge mud bottoms and on-ridge shell ridges. Exploitation of different resources reduces competition (Keast and Webb 1966, Wikramanayake 1990, Hyndes *et al*. 1997) among juveniles and introduces new nutrition sources into the diet that can be advantageous to fast growth, which is vital to juvenile survival. Juvenile red snapper growth rates differ significantly between on- and off-ridge habitats (Szedlmayer and Conti 1999, Rooker *et al.* 2004). Specifically, juvenile growth rates were significantly higher in off-ridge areas from Freeport Rocks (Rooker *et al.* 2004, Geary *et al*. in press). This elicits several questions. Are differences in growth rates a reflection of differences in prey composition of juveniles? Would variation in prey composition be a result of different ontogenetic development of juveniles between the two habitats, or do juveniles to adapt to prey availability by altering feeding morphology or modulating feeding behavior?

Morphology and behavioral performance influence one another as well as the ecological patterns of an organism. Morphology and feeding performance limit the ability of an individual to exploit its surrounding resources, such as its ability to capture and handle prey items, which shapes the individual's foraging ecology by determining what resources can be included in the diet.

Ecological Morphology of Teleost Feeding

Ecomorphological studies are predicated on identifying patterns among morphology, behavioral performance, and ecology. Ecomorphological methods have been utilized in past studies to test a variety of hypotheses concerning the relationships between feeding performance and foraging ecology among teleosts (e.g. Keast and Webb 1966, Motta 1988, Wainwright and Richard 1995, Wainwright 1996, Grubrich 2000, and Svanbäck *et al*. 2002). Ultimately, feeding performance can affect fitness through effective energy consumption that can be directed towards growth and reproduction (Arnold 1983, Nagelkerke and Sibbing 1996, Wainwright 1996, Svanbäck and Eklöv 2003). Fast growth is most advantageous during larval and juvenile stages when individuals are most vulnerable to predation (Werner and Gilliam 1984, Post 2003). Taking advantage of the most abundant or energetic food source as a juvenile increases survival and enhances recruitment potential.

Methods in which fish obtain their resources are highly variable, but can be generalized into three major types of prey capture, 1) ram feeding; a method in which prey is overtaken by an actively swimming predator, 2) biting; using jaws to bite pieces of prey or remove prey attached to substrates, and 3) suction; the most common method, a rapid expansion of the buccal cavity resulting in a negative pressure that draws water and prey into the predators' mouth (Liem 1993, Norton 1995). Species can specialize in capturing particular prey, or can exhibit a more generalized prey capture method. Specialization is

advantageous in static environments, with constant prey composition. However, in a dynamic environment with changing prey composition, generalists are at an advantage since they can consume a variety of prey types (King 1971, Liem 1980, Luczkovich *et al.* 1995). The more general the prey capture method, the wider niche an individual can presumably occupy (Luczkovich *et al*. 1995). Therefore, the ecological niche of an individual can be shaped by the morphological and behavioral characteristics of its feeding apparatus. The unique versatility of the teleost skull provides fish the ability to modulate feeding behavior in response to prey variability (Nemeth 1997, Cutwa and Turingan 2000, Ferry-Graham *et al.* 2001), or change their feeding behavior through ontogeny (Osenberg *et al.* 1988, Wainwright 1988, Galis 1993, Wainwright and Richard 1995, Hunt von Herbing 2001). Many fishes exhibit an ontogenetic shift in prey that corresponds to a change in their feeding morphology and behavior (Stoner 1980, Eggold and Motta 1992, Luczkovich *et al.* 1995, Wainwright and Richard 1995, Hernandez and Motta 1997, Monteiro *et al*. 2005). Such changes can initiate resource partitioning, ontogenetically (Hernandez and Motta 1997, Grubich 2005) or interspecifically (Mittelbach *et al.* 1992, Aerts and DeVree 1993, Galis 1993, Nagelkerke and Sibbing 1996, Huskey and Turingan 2001).

Red snapper were the target species for this study. Although red snapper larval development (Collins *et al*. 1980, Pothoff *et al*. 1988, Drass *et al*. 2000) and stomach contents (adult and juvenile) (Bradley and Bryan 1976, Moran 1988, Ouzts and Szedlmayer 2003, Szedlmayer and Lee 2004) have been

examined, their feeding mechanics and behavior has not been investigated. Therefore, the goal of this research is to explore the relationships between morphology, behavioral performance, and trophic ecology of juvenile red snapper, and determine how these interactions may influence growth and settlement patterns. These relationships will be examined by modeling the biomechanics of juvenile jaws and measuring feeding performance, shape differences, and diet differences to determine whether juvenile red snapper alter their feeding morphology or behavior over ontogeny or between two selected habitats, and if these differences are reflected in their actual diet.

Lower Jaw Lever Mechanics

Biomechanical models are useful tools in investigating morphological variation in a functional context. Models have successfully been used in several teleost feeding studies to predict feeding performance (Westneat 1991, 1994, 2004, Carroll *et al*. 2004, Grubich 2005, Van Wassenbergh *et al*. 2005). The biomechanics of red snapper feeding can be modeled by investigating the anatomical arrangement of the lower jaw as a 3rd order lever, where the effort (the force applied to the lever) and load (the force exerted by the lever) are on the same side of the fulcrum, with effort being the closest to the fulcrum (Westneat 2003, 2004). Lever mechanics can be used to calculate the trade off between velocity and force (Wainwright and Richard 1995, Westneat 2003) and consequently make predictions about red snapper feeding mode. This forms a theoretical niche in which red snapper may potentially operate. Conducting

actual feeding performance studies can test predictions of feeding mode, as well as the accuracy of the model itself.

Feeding Performance

Feeding performance can be characterized and quantified by kinematic analyses. Red snapper feeding performance is as equally important as feeding morphology in shaping diet composition. Variations in morphology can affect feeding performance by physically modifying or releasing the morphological constraints in which a fish can operate (Keast and Webb 1966, Motta 1988, Wainwright 1996, Waltzek and Wainwright 2003). Alternatively, performance can differ as a response to variation in prey item and composition. Differences identified in feeding performance may allow a species or particular size class to exploit one resource over another (Wainwright 1996). Comparing physiological data of red snapper to actual diet composition will determine if variations in diet are a result of differences in red snapper performance.

Phenotypic Variation

Shape analysis, or geometric morphometry, quantifies variation in shape among individuals or populations in relation to changes due to growth or different ecological conditions. Shape analysis is useful for discriminating between the effects of the factor of interest. Traditionally multivariate analyses of linear measurements taken across the body form were used to quantify shape. Recently, geometric morphometrics has been used, which analyzes the geometry of shape across landmark locations rather than linear distances. This

method has been shown to be more accurate in distinguishing shape differences (Parsons *et al*. 2003). Deformation grids generated using geometric morphometrics can provide visual interpretations of results (Parsons *et al*. 2003, Parsons and Robinson in press).

This study will explore the adaptive phenotypic plasticity response of juvenile red snapper between two habitats. Phenotypic plasticity is the expression of phenotypes that are dependent upon ontogenetic development (Svanbäck and Eklöv 2002) and variations in environmental factors. Habitat has been shown to generate resource polymorphism in fish, where fish of the same species but from different habitats developed different body shapes, and therefore the ability to consume different prey types (Lavin and McPhail 1986, Ehlinger and Wilson 1988, Malmquist 1992, Robinson *et al*. 1996, Svanbäck and Eklöv 2002). Differences in head and body shape of juvenile red snapper would provide further information on differences in feeding morphology and behavior.

Stomach Contents

Information regarding the feeding habits of juvenile red snapper is essential in understanding their life history and trophic requirements. Numerous studies have used stomach content analyses to qualitatively and quantitatively characterize the natural feeding habits of various teleost species (*e.g.* Grossman 1980, Moyle and Senanayake 1984, Eggold and Motta 1992, Platell *et al*. 1998, Reichert 2003, Szedlmayer and Lee 2004). Stomach content analysis can determine actual patterns of resource use in juvenile red snapper. Through

stomach content analysis it is also possible to determine if there are any substantial differences in resource use, or resource partitioning, among size classes or between habitats, which may be related to feeding biomechanics. Comparisons can be made across individuals to determine if feeding ecology varies due to morphology or behavior, to quantify the presence of ontogenetic shifts in diet, and quantify any dietary overlap either among size classes or between habitats.

Hypotheses

Ecomorphological approaches will be used to explore the relationships between ecology and morphology of juvenile red snapper. These relationships will be used to describe the influence ontogeny and habitat variation has on shaping a juveniles' ability to exploit resources, and provide insight into essential fish habitat of juveniles. This will be accomplished by testing the following hypotheses:

H_o 1: There is no significant difference in the morphology of the feeding apparatus of juvenile red snapper across ontogeny or between two types of habitat. This hypothesis will be tested by modeling the lower jaw as a class III lever to make predictions concerning the timing, force production, and velocity transmission during the closing of the lower jaw. The accuracy of these predictions will be tested using actual feeding events.

H_o 2: There is no significant difference between predicted model output and output from actual feeding events of juvenile red snapper. Kinematic trials of

juvenile red snapper will test the validity of the lower jaw model. If no significant difference is found then the model is an accurate predictor of feeding behavior of juvenile red snapper.

H_o 3: There is no significant difference in feeding performance across ontogeny or between two types of habitat of juvenile red snapper. Feeding performance of juveniles from each habitat will be measured by recording actual feeding events of juveniles and calculating displacement, angular, and velocity variables of jaw movement.

H_o 4: There is no significant difference in the head and body shape of juvenile red snapper across ontogeny or between two types of habitat. Geometric morphometrics will be used to compare head and body shape variations in juveniles over ontogeny and determine if juvenile red snapper exhibit phenotypic plasticity as a result of habitat.

H_o 5: There is no significant difference in stomach contents of juvenile red snapper across ontogeny or between two types of habitat. Stomach content analysis will determine patterns of resource use in juveniles. Actual resource use will then be compared to predictions made from previous hypotheses.

METHODS

Animal Collection

Juvenile red snapper were collected between June and September 2004, and in August 2005, on and off the Freeport rocks shell ridge, Texas. On-ridge areas were characterized by abundant relic oyster shell presence and off-ridge sites were characterized by silt and mud. Juvenile red snapper (n = 601) were collected using a 6-meter otter trawl with 2 cm mesh, 1.25 cm inner mesh, 0.6 cm link tickler chain, and 18 x 36 inch doors. Trawls were made in 5-minute increments at 2.5 knots. Juveniles for performance studies were sorted by habitat (on-ridge and off-ridge) and kept in separate live wells onboard the research vessel. Fish that were trawled up dead were frozen and kept for morphological and gut content analysis. Mass (g) and standard length (SL) (cm) were recorded for all juveniles and the following size classes assigned, small (1.8-3.9 cm SL), medium (4.0-5.9 cm SL), or large (6.0-10.88 cm SL). Collections were made under TAMU Animal Use Protocol #2003-84 and Texas Park and Wildlife Permit # SPR 0902-243.

General Statistics

Prior to conducting parametric tests, normality of the data was tested using a Kolmogorov-Smirnov test. If normality was not met, data were transformed. Levene's test was used to test the assumption of homogeneity of variances. Bonferroni post-hoc tests were used when the assumption of equal variance was met; Dunnett's t3 post-hoc tests were used in cases where variances were

heteroscedastic. All statistical tests were conducted using SPSS 11 for a Mac and JMP 6 (SAS).

Model of Lower Jaw Lever Mechanics

The program MandibLever 3.2 (Westneat 2003) was used to model the lower jaw in juvenile red snapper. This model incorporates the influence of closing muscles on lever ratio calculations and creates a set of dynamic output variables over the entire jaw closing. Previous jaw lever mechanical studies (Wainwright and Richard 1995, Westneat 1994, 2004) used static values of mechanical advantage, which were derived from the ratio of input to output levers, as a reference to the force a fish can produce. The reciprocal of mechanical advantage is the velocity ratio, a reference to the speed at which a fish can move its jaws. Therefore, mechanical advantage and velocity are biomechanical trade-offs, where strong jaws are slow and visa versa. The use of a dynamic model is advantageous since static measurements usually over estimate mechanical advantage because the influence of changing muscle insertion angles is not accounted for (Westneat 2003). The model, therefore, calculates an effective mechanical advantage (EMA), which is a more accurate measurement of force translation of the lower jaw. The model also calculates a variety of other dynamic variables, such as force, angular velocity, and percent muscle contraction, and these parameters can be used to make predictions regarding fish feeding performance.

Lever mechanics were used to determine the trade-offs between force and velocity when closing the lower jaw and to make predictions regarding prey acquisition patterns in juvenile red snapper. First, exploratory dissections of juvenile heads were conducted (n = 5), skeletons prepared (n = 5), and individuals cleared and stained (n = 5) (Taylor and Van Dyke 1985) in order to characterize the cranial skeletal and muscular elements associated with feeding (Figs. 1&2). Then, for the remaining juveniles (n = 230), twelve morphometric measurements of the lower jaw and associated jaw closing muscles, the A2 and A3 subdivisions of the adductor mandibulae, (Table 1, Fig. 2) were taken to the nearest 0.01 cm using either a calibrated eye reticle on a Nikon SMZ1500 stereoscope, or with digital vernier calipers and muscle weight to the nearest 0.01 g. Assumptions about jaw muscle contractile physiology were made (following Westneat 2003): jaw opening rotation (57 degrees) (based on juvenile red snapper kinematic data), jaw opening duration (30 ms), force per unit area of muscle contraction (200 kPa), unloaded shortening velocity of muscle (Vmax, 10 lengths/s), minimum shortening velocity, (V/Vmax, 0.05), range of peak V/Vmax (0.05-0.8), and the widest simulated range of F/Fmax calculated from muscle velocity using the Hill equation (0.05-0.79). Morphometric measurements and muscular assumptions were used as inputs in the biomechanical lever model. Simulations of lower jaw closing were run for individuals to predict feeding behavior of juvenile red snapper from three size classes and two habitats.

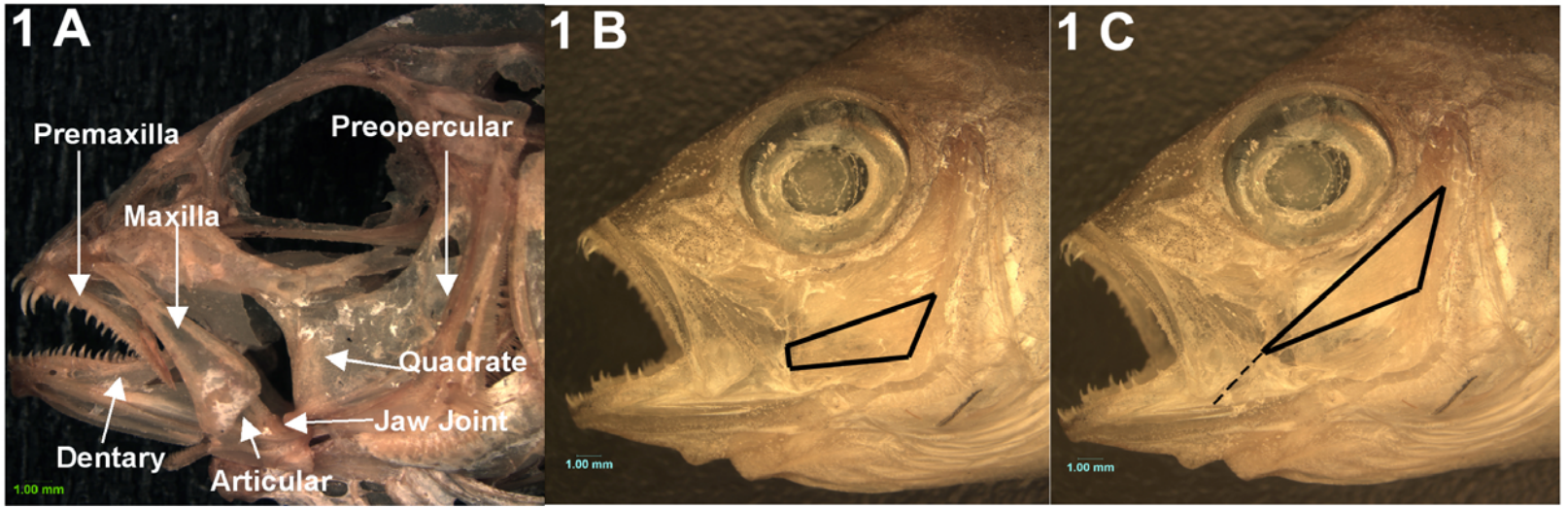

Figure 1. Cranial skeletal and muscular elements of juvenile red snapper. (A) Cranial osteology associated with feeding. (B) Adductor mandibulae subdivision A2, which originates on the preopercle and inserts on the coronoid process. (C) Adductor mandibulae subdivision A3, which originates on the hyomandibula and inserts on the medial surface of the lower jaw.

Table 1. Morphometric data used as input into the lever model, MandibLever 3.2. Mean values (±S.E.M.) for juvenile red snapper from three size classes and two habitats.

	Small (n = 74)	Medium (n = 82)	Large (n = 74)	On-ridge (n = 113)	Off-ridge (n = 117)
1. Inlever A2 (cm)	0.13 (±0.01)	0.21 (±0.01)	0.29 (±0.01)	0.20 (±0.01)	0.22 (±0.01)
2. Inlever A3 (cm)	0.19 (±0.01)	0.31 (±0.01)	0.42 (±0.01)	0.32 (±0.01)	0.29 (±0.01)
3. Inlever Open (cm)	0.08 (±0.003)	0.12 (±0.003)	0.18 (±0.004)	0.13 (±0.005)	0.12 (±0.004)
4. Outlever (cm)	0.59 (±0.01)	0.87 (±0.01)	1.21 (±0.01)	0.95 (±0.02)	0.83 (±0.03)
5. A2 length (cm)	0.34 (±0.01)	0.52 (±0.01)	0.75 (±0.01)	0.58 (±0.02)	0.49 (±0.02)
6. A3 total length (cm)	0.57 (±0.01)	0.94 (±0.02)	1.38 (±0.02)	1.03 (±0.03)	0.90 (±0.03)
7. A3 tendon length (cm)	0.12 (±0.004)	0.69 (±0.33)	0.35 (±0.01)	0.58 (±0.24)	0.22 (±0.01)
8. A2-joint distance (cm)	0.32 (±0.01)	0.49 (±0.01)	0.70 (±0.01)	0.54 (±0.02)	0.46 (±0.02)
9. A3-joint distance (cm)	0.55 (±0.01)	0.85 (±0.01)	1.24 (±0.02)	0.93 (±0.03)	0.83 (±0.03)
10. A2-A3Ins (cm)	0.12 (±0.004)	0.21 (±0.004)	0.29 (±0.01)	0.21 (±0.01)	0.20 (±0.01)
11. LJtop length (cm)	0.51 (±0.01)	0.73 (±0.01)	1.02 (±0.01)	0.82 (±0.02)	0.69 (±0.02)
12. LJBot length (cm)	0.65 (±0.01)	0.96 (±0.01)	1.33 (±0.02)	1.04 (±0.03)	0.92 (±0.03)
13. A2 Mass (g)	0.001 (±0.0001)	0.003 (±0.0002)	0.01 (±0.001)	0.005 (±0.0004)	0.003 (±0.0004)
14. A3 Mass (g)	0.001 (±0.0001)	0.004 (±0.0002)	0.02 (±0.003)	0.01 (±0.002)	0.01 (±0.001)

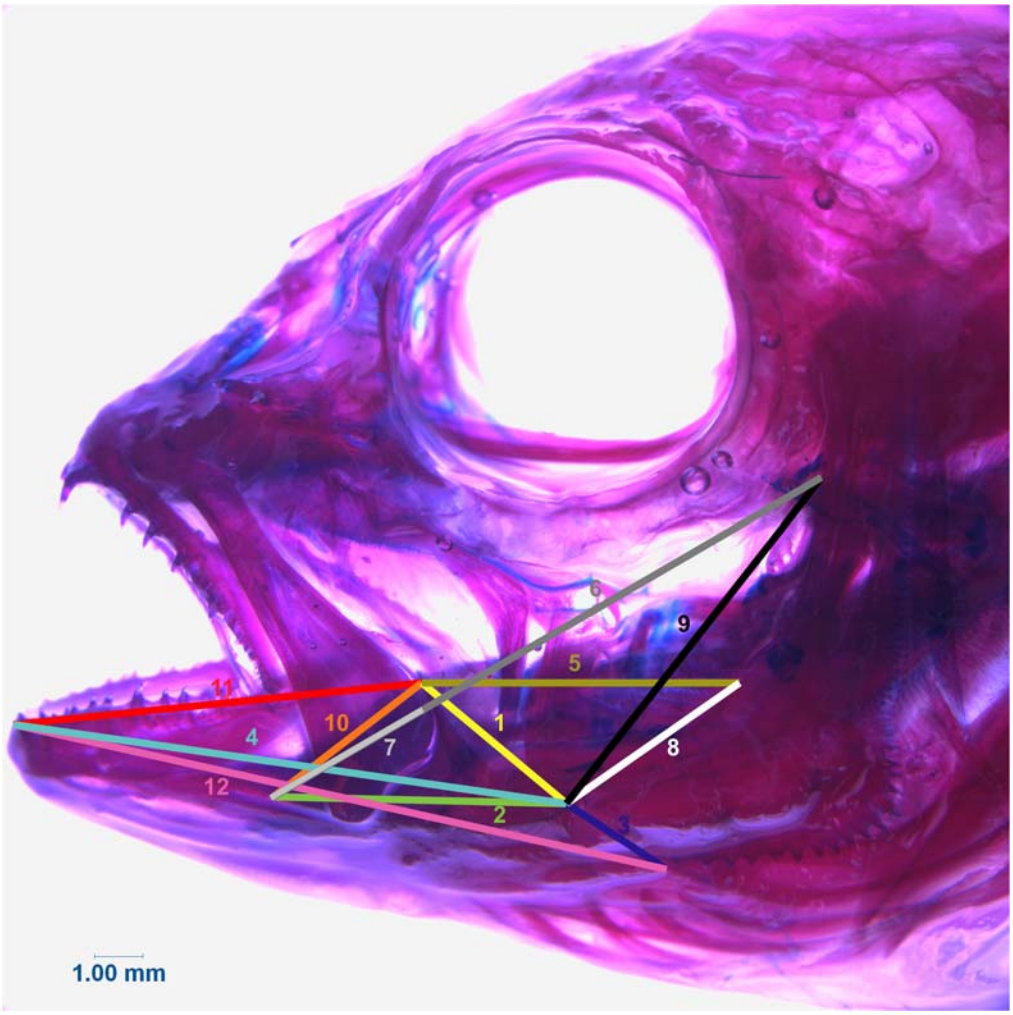

Figure 2. Morphometric measurements used as inputs in the jaw lever model, MandibLever 3.2. (1) Inlever A2, from quadrate-articular joint to A2 insertion point on ascending process of articular; (2) Inlever A3, from quadrate-articular joint to A3 insertion point on medial face of lower jaw; (3) Inlever Open, from quadrate-articular joint to insertion of interoperculomandibular ligament on posteroventral margin of articular; (4) Outlever, from quadrate-articular joint to anterior most tip of dentary; (5) A2 length, from origin on ventral margin on preopercle to insertion on ascending process of articular; (6) A3 total length, from origin on preopercle and hyomandibula to insertion on medial face of lower jaw; (7) A3 tendon length, from origin on tapering end of A3 muscle to insertion on the medial face of the lower jaw; (8) A2-joint distance, distance from A2 origin to quadrate-articular joint; (9) A3-joint distance, distance from A3 origin to quadrate-articular joint; (10) A2-A3 ins, distance from A2 insertion to A3 insertion; (11) LJtop length, from the tip of the coronoid process to anterior jaw tip; (12) LJBot length, from the posteroventral margin of articular to anterior jaw tip.

To test the hypothesis that there is no significant difference in the morphology of the feeding apparatus of juvenile red snapper across ontogeny, output parameters were analyzed using multivariate analyses of variance (MANOVA) with size class as a fixed factor and model output parameters as dependent variables. Significant differences among size classes were determined by post-hoc tests. To test for significant differences between habitats, output parameters were analyzed using multivariate analyses of covariance (MANCOVA) with habitat as a fixed factor, model output parameters as dependent variables, and standard length as a covariate.

Feeding Performance

Behavioral performance was used to validate the predictive biomechanical model output, and compare the feeding biomechanics of juvenile red snapper across size classes and between habitats. Juvenile red snapper (n = 448) were transported to the laboratory and housed in habitat specific 10-50 gallon saltwater tanks and maintained at 26 °C, 32 ppt (salinity), 8.2 pH. Fish were allowed to acclimate and then trained to feed from a small section of stationary tubing under 500 watts of lighting (Fig. 3). During the first collection season, a mass mortality event occurred due to an *Amyloodinium ocellateum* outbreak and hurricane evacuations. Therefore, not enough individuals were available to examine ontogenetic changes, and so only habitat is included in kinematic analysis. Juveniles used in feeding performance trials were all within the same size class (4.0-5.9 cm SL).

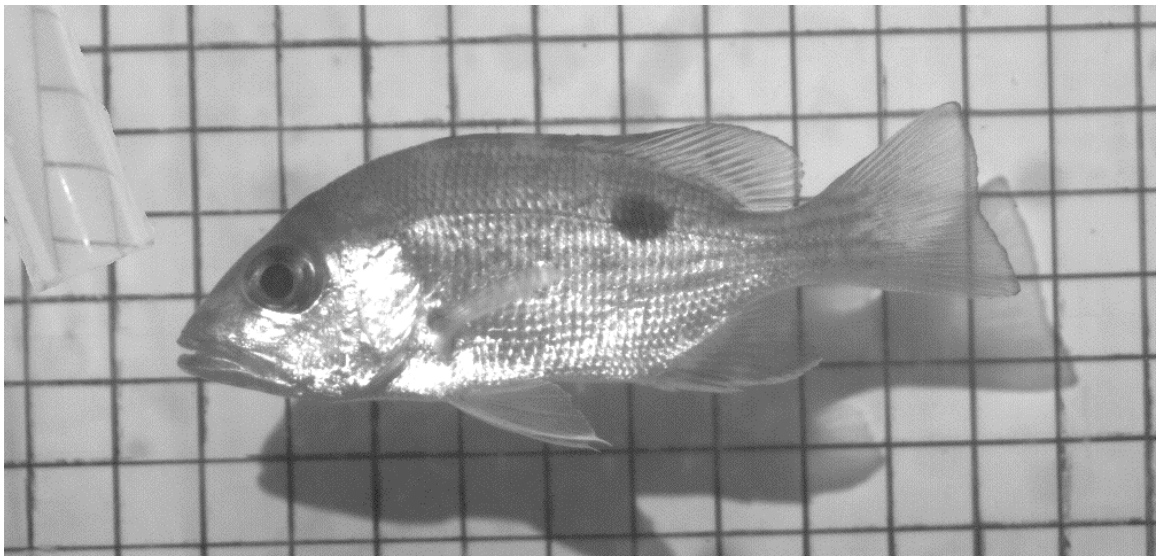

Figure 3. Image of experimental setup.

During feeding trials juveniles were positioned laterally in front of the camera using a piece of plexiglass with a $1cm^2$ grid as a reference and fed pieces of squid, sized to 50% of the individual's oral diameter, until satiated. Feeding events were recorded using a Redlake PCI Motion Scope high-speed camera at 250 frames s^{-1}. Perpendicular orientation to the camera lens and fully ingested prey were used as criteria for inclusion of feeding events in the analyses. Three feeding events for each juvenile were selected for analysis. Juveniles were then sacrificed with an overdose of MS-222.

Feeding events from 8 on-ridge and 9 off-ridge juveniles were digitized frame by frame, starting with the onset of strike until mouthparts returned to their starting position, using Motus 8.2 (Peak Performance, Inc., Denver, CO), in which 11 anatomical landmarks (Fig. 4) were used to calculate the following 15 kinematic variables (following Westneat 1990, 1994 and Gibb 1995, 1996, 1997): (1) maximum gape (cm), the maximum distance between the anterior regions of the premaxilla and dentary; (2) time to maximum gape (ms), the interval between initial mouth opening and maximum gape; (3) maximum gape angle (degrees), the angle measured from the anterior tip of the premaxilla to the maxilla-premaxilla articulation (vertex) to the anterior tip of the dentary; (4) time to maximum gape angle (ms), the interval between initial mouth opening and maximum gape angle; (5) maximum lower jaw rotation (degrees), maximum calculated angle from the anterior tip of the dentary to the mandible/quadrate

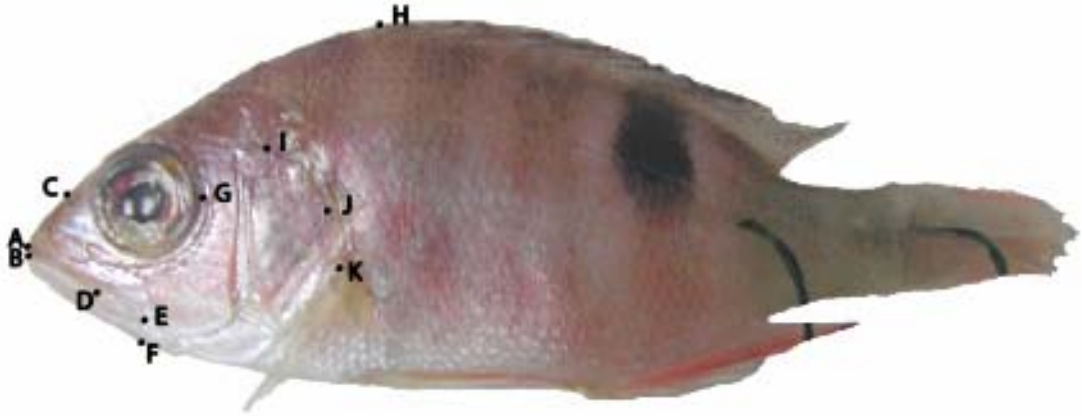

Figure 4. Points used for digitizing juvenile red snapper cranial kinematics from feeding trials. (A) anterior tip of premaxilla, (B) anterior tip of dentary, (C) dorsal most visible point of maxilla, (D) maxilla-premaxilla articulation, (E) mandible/quadrate articulation, (F) ventral floor of mouth, (G) posterior-most point of orbit of eye, (H) first dorsal spine origin, (I) anterodorsal tip of opercle at junction with preopercle and hyomandibula, (J) posterodorsal tip of opercle, (K) origin of first pectoral fin ray.

articulation (vertex) to the origin of the pectoral fin; (6) time to maximum lower jaw rotation (ms), the interval between initial mouth opening and maximum lower jaw depression; (7) maximum upper jaw protrusion (cm), maximum distance from the posterior most point on the eye and the anterior tip of the premaxilla; (8) time to maximum upper jaw protrusion (ms), the interval between initial mouth opening and maximum upper jaw protrusion; (9) maximum cranial rotation (degrees), the angle measured from the dorsal most visible point of the maxilla to the first dorsal spine origin (vertex) to the origin of the first pectoral fin ray; (10) time to maximum cranial rotation (ms), the interval between initial mouth opening and maximum dorsal rotation of the neurocranium; (11) maximum depression of the hyoid (cm), maximum distance between the posterior most point on the eye and the ventral floor of the mouth; (12) time to maximum hyoid depression, the interval between initial mouth opening to maximum hyoid depression; (13) maximum maxillary rotation (degrees), the angle measured from the maxilla-premaxilla articulation to the dorsal most visible point of maxilla (vertex) to the first dorsal spine origin; (14) time to maximum maxillary rotation (ms), the interval between initial mouth opening and maximum maxillary rotation; and (15) length of gape cycle (ms), total time the mouth is open during the feeding event. Angular velocities and phase timings were also calculated.

The kinematic variables, gape distance and gape angle velocity, were used to validate the predictive ability of the lever model (following Westneat 1994). Linear regressions were used to test the linearity of the independent variable

(lower jaw rotation) versus the dependent variables (gape distance and gape angle velocity). If the results had a linear relationship then an ANCOVA was used to test significant differences between the slopes of the regression lines from video kinematics and model predictions. If no significant differences were found then the model was considered to be an accurate predictor of feeding behavior. Percent error of the model in predicting feeding behavior was also calculated. The maximum value of lower jaw rotation from actual feeding events was multiplied by the regression slopes of each line for gape distance and gape angle velocity from the video and model results. These products calculated estimated dependent variables that were used in the following equation to calculate percent error.

$$\frac{\text{(estimated value for the model)} - \text{(estimated value for video)}}{\text{(estimated value for the model)}} \times 100 \qquad (1)$$

Kinematic variables were also used to characterize and quantify the feeding behavior of juvenile red snapper between habitats. Independent t-tests were used to test the hypothesis that there is no significant difference between habitats for each of the kinematic variables ($\alpha = 0.05$). Kinematic profiles were generated for each variable to examine their relationship to one another and identify different phases over a complete feeding event. Kinematic timing variables and time to prey capture were analyzed using paired t-tests to examine the relationships between time to maximum kinematic values and time to capture prey.

Phenotypic Variation

Landmark-based geometric morphometrics uses landmark coordinates to record positional information about the individual. Landmarks used were homologous, consistent in position, provided adequate coverage of the morphology of the organism, reliable and repeatable, and all laid within the same plane (Zelditch *et al*. 2004). Algebraic calculations were then used to remove differences between these landmarks attributed to location, scale, and orientation, leaving only shape differences (Zelditch *et al*. 2004). These remaining shape differences were used to test hypotheses related to habitat and ontogenetic effects on shape.

Lateral images of juvenile red snapper (n = 111) were captured using a Nikon CoolPix 885 digital camera. Two-dimensional coordinates were recorded from 19 landmarks digitized around the juvenile body perimeter using the program tpsDig (V. 2, Rohlf 2005a). Landmarks included: (1) anterior tip of dentary; (2) anterior tip of premaxilla; (3) anterior-most point of eye orbit; (4) center of eye; (5) posterior-most point of eye orbit; (6) top of head where skull breaks away from body outline; (7, 8) anterior and posterior insertions of the dorsal fin, respectively, (9) dorsal origin of the caudal fin, (10) middle of the caudal fin insertion where lateral line terminates; (11) ventral origin of the caudal fin; (12, 13) posterior and anterior insertions of the anal fin, respectively; (14) anterior-most insertion of the pelvic fin; (15) first branchiostegal ray at the body

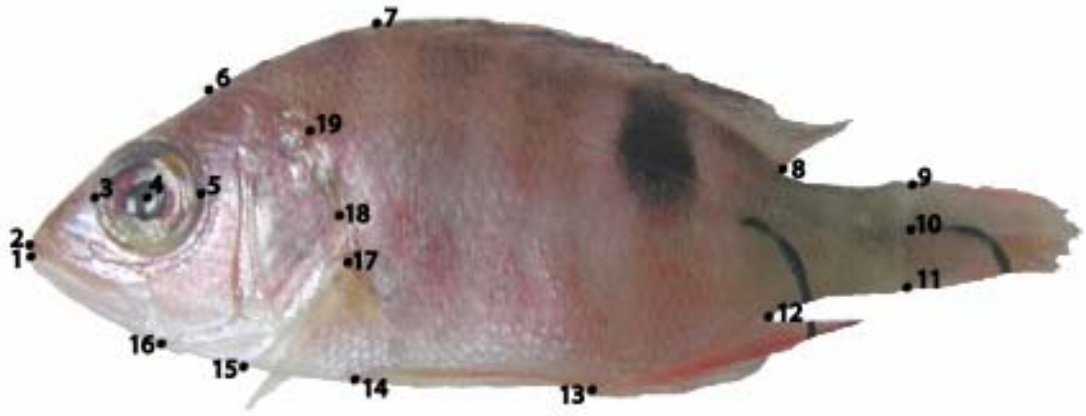

Figure 5. Landmark configuration on juvenile red snapper used in morphometric analysis. (1) anterior tip of dentary, (2) anterior tip of premaxilla, (3) anterior-most point of eye orbit, (4) center of eye, (5) posterior-most point of eye orbit, (6) top of head where skull breaks away from body outline, (7, 8) anterior and posterior insertions of the dorsal fin, respectively, (9) dorsal origin of the caudal fin, (10) middle of caudal fin insertion where lateral line terminates, (11) ventral origin of caudal fin, (12, 13) posterior and anterior insertions of the anal fin, respectively, (14) anterior-most insertion of the pelvic fin, (15) first branchiostegal ray at the body outline, (16) quadrate-articular joint, (17) origin of first pectoral fin ray, (18) posterodorsal tip of opercle, (19) anterior-most point of the lateral line.

outline; (16) quadrate-articular joint; (17) origin of first pectoral fin ray; (18) posterodorsal point of opercle; (19) anterior-most point of the lateral line (Fig. 5). TpsRelw software (v. 1.42, Rohlf 2005b) aligned shape data by rotating, translating, and scaling the landmark coordinates, using least squares superimposition. Aligned data were used to calculate shape variables that were used in statistical analyses. Significant variations in shape were tested using MANOVA with shape variables as dependent variables and habitat and shape as fixed variables. An eigendecomposition of the effect Sum of Squares and Cross-Products (SSCP) matrix was performed and used to calculate the shape variance explained by habitat and allometry. In addition, associated eigenvectors were multiplied by shape variables to yield linear axis scores. TpsRegr software (v. 1.31, Rohlf, 2003) produced thin-plate spline transformation grids, which provided a visualization of shape variation. Transformation grids were magnified 10-fold to enhance key morphological differences.

Stomach Content Analysis

Dietary data were used to characterize the diet of juvenile red snapper, quantify prey composition among size classes and between habitats, and to confirm dietary patterns with feeding morphology and kinematics. Stomachs were removed at the junction of the esophagus to the first bend of the intestines (McCormick 1998), from juvenile red snapper (n = 173) and weighed. Stomachs were stored in 10% formalin until analysis. Stomach contents were placed in a

petri dish with a drop of rose Bengal stain, to aid in prey identification, and examined under a Nikon SMZ1500 stereoscope. Contents were counted, weighed, and identified to the lowest taxonomic group possible. A two-factor ANOVA tested the hypothesis that there was no difference in prey composition among size classes and between habitats ($\alpha = 0.05$). These results were then compared to the predictions made using morphometric and kinematic analysis to determine if predicted diet coincided with the observed diet.

RESULTS

Lower Jaw Lever Model

Ontogeny

Model simulations demonstrated that the potential actions of the A2 and A3 subdivisions of the adductor mandibulae changed over ontogeny in juvenile red snapper. Effective mechanical advantage increased and velocity ratio significantly decreased for both the A2 and A3 muscles as body size increased (Table 2, Fig. 6). Muscle force contribution and total bite force significantly increased with body size (Table 2, Fig. 7). As gape increased with size, closing duration significantly decreased resulting in an expected significant increase in angular velocity (Table 2, Fig. 8A-C). Percent muscle contraction required to close the lower jaw decreased over ontogeny (Table 2, Fig. 8D).

The potential roles of the A2 and A3 muscles changed as juvenile red snapper grew and increased in size. The difference between A2 and A3 muscle force contribution and bite force became greater in large juveniles (Fig. 7 A,B). The difference in jaw closing durations between the A2 and A3 muscles decreased as body size increased. Specifically, the A2 muscle closing duration increased while the A3 muscle duration decreased (Fig. 8B). The A2 muscle angular velocity was faster than the A3 muscle in small juveniles, but slower than the A3 muscle in medium and large juveniles (Fig 8C).

Table 2. Results of A2 and A3 muscle parameters from lever model simulations of lower jaw closing for juvenile red snapper.

Ontogeny

		Length (cm)	CSA (cm2)	EMA	VR	Fact (N)	BiteF (N)	Dur (ms)	Gape (cm)	AngVel (o/ms)	% Cont
A2	Small	0.56	0.002	0.21	4.83	0.03	0.01	89.8	0.52	3.41	21.2
	Medium	0.91	0.01	0.22	4.5	0.07	0.02	91.1	0.76	3.55	21.6
	Large	1.14	0.01	0.22	4.56	0.18	0.04	87.7	1.06	3.82	20.8
A3	Small	0.71	0.003	0.31	3.13	0.04	0.01	98.4	0.52	3.31	23.3
	Medium	1.12	0.01	0.32	2.89	0.09	0.03	94.6	0.75	3.99	22.4
	Large	1.62	0.02	0.32	2.92	0.27	0.08	90.1	1.05	3.95	21.3

Habitat

		Length (cm)	CSA (cm2)	EMA	VR	Fact (N)	BiteF (N)	Dur (ms)	Gape (cm)	AngVel (o/ms)	% Cont
A2	On-ridge	0.71	0.01	0.19	5.15	0.11	0.02	79.4	0.83	4.25	18.8
	Off-ridge	1.03	0.01	0.24	4.12	0.08	0.02	99.4	0.73	2.96	23.5
A3	On-ridge	1.21	0.01	0.3	3.03	0.17	0.05	91.6	0.82	4.07	21.7
	Off-ridge	1.08	0.01	0.32	2.93	0.11	0.03	97.2	0.72	3.46	23.0

Parameter abbreviations are as follows: muscle length (length), cross-sectional area (CSA), effective mechanical advantage (EMA), velocity ratio (VR), muscle force exerted (Fact), muscle bite force contribution (BiteF), closing duration (Dur), closing gape distance (Gape), angular velocity (AngVel), percent muscle contraction required to close the lower jaw (% Cont).

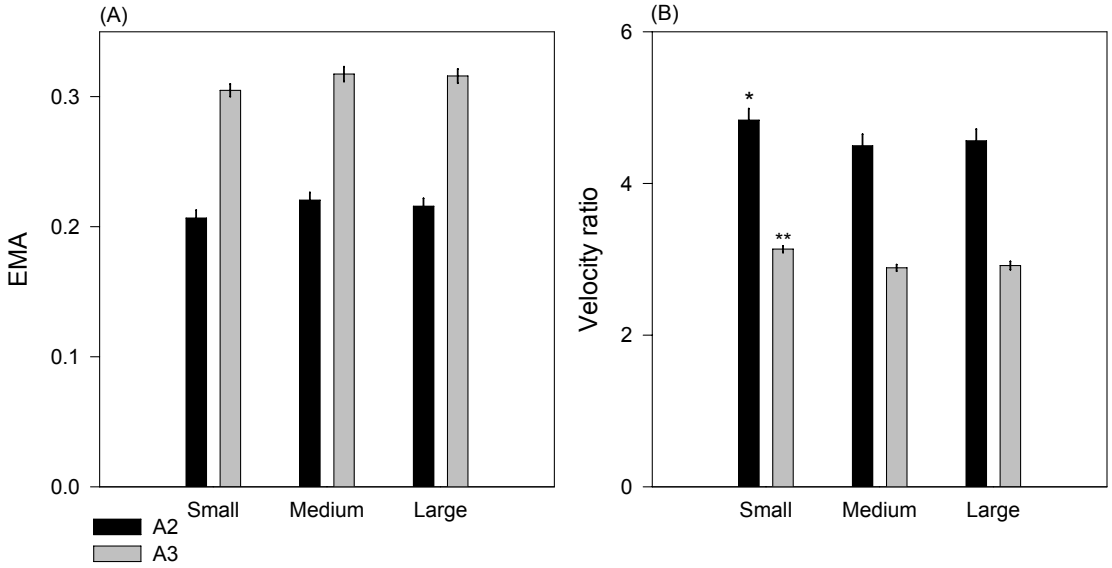

Figure 6. Mean (± S.E.M.) simulation results from the lever model, MandibLever 3.2. (A) Effective mechanical advantage and (B) velocity ratio for the A2 and A3 muscles from three size classes of juvenile red snapper.
* A2 muscle $p < 0.05$
** A3 muscle $p < 0.01$

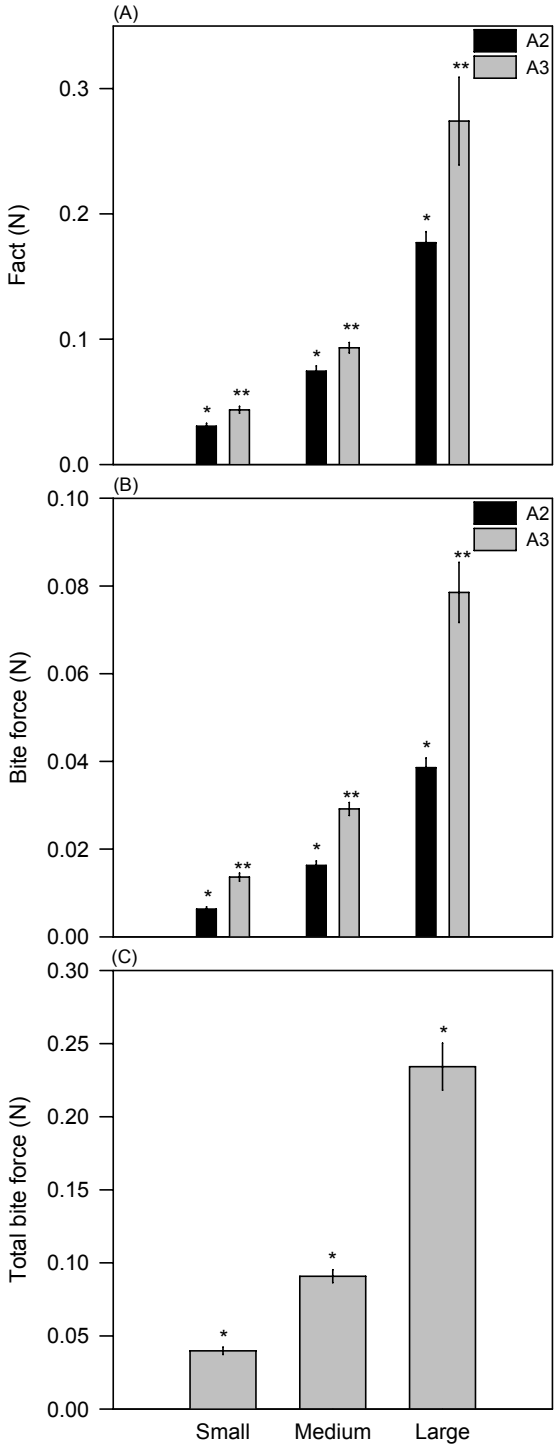

Figure 7. Mean (± S.E.M.) simulation results of lower jaw closing from the lever model for three size classes of juvenile red snapper. (A) Muscle force exerted (Fact), (B) bite force contribution (Bite F) of the A2 and A3 muscles, and (C) total bite force.
* A2 muscle $p < 0.01$ (A, B), total bite force $p < 0.01$ (C)
** A3 muscle $p < 0.01$ (A, B)

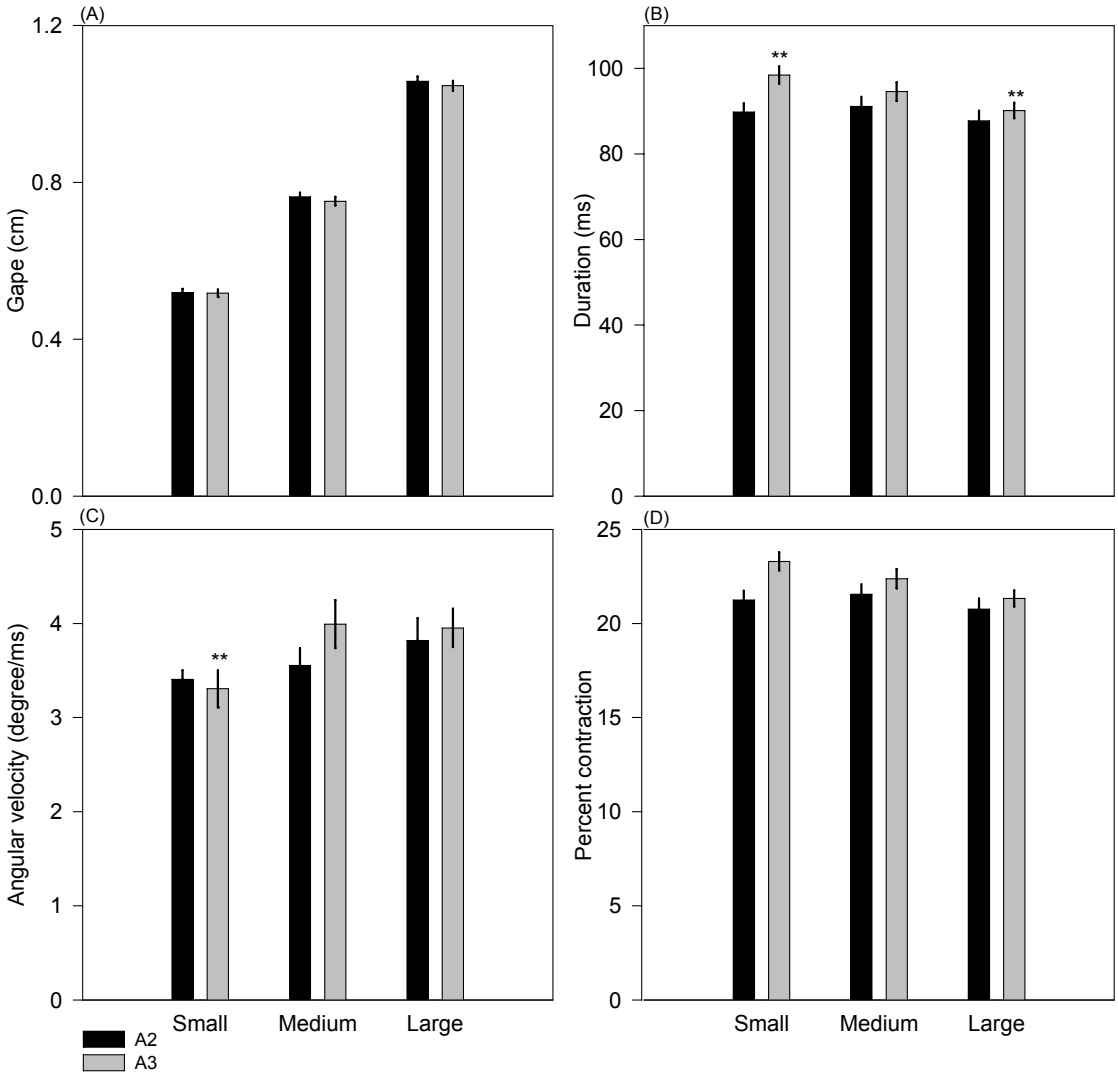

Figure 8. Mean (± S.E.M.) simulation results of lower jaw closing from the lever model for three size classes of juvenile red snapper. (A) Gape change, (B) duration of lower jaw closing, (C) angular velocity of the lower jaw, and (D) percent contraction required to close the lower jaw.
* A2 muscle $p < 0.05$
** A3 muscle $p < 0.05$

The percent muscle contraction of the A2 muscle required to close the lower jaw remained approximately the same across all size classes, but decreased continually for the A3 muscle (Fig. 8D).

Habitat

Model simulations were run for juveniles from the two habitats, pooling size classes together, to determine if A2 and A3 muscle function differed between habitats. Multivariate tests, with size (SL) as a covariate, were used to test for significant differences in muscle morphology and model output between on-ridge and off-ridge habitats. The cross-sectional areas of the A2 and A3 muscles in juveniles did not differ significantly between habitats (Table 2). Muscle lengths differed between habitats; the A2 muscle was longer in off-ridge juveniles and the A3 muscle was longer in on-ridge juveniles (Table 2). Velocity ratios of the A2 and A3 muscles were significantly greater and effective mechanical advantage (EMA) was significantly less in on-ridge juveniles compared to off-ridge juveniles. The A2 muscle had greater velocity and lower EMA than the A3 muscle for both habitats (Fig. 9). Muscle force contribution to bite force and total bite force was not significant between habitats; the A3 muscle had greater force than the A2 muscle for both habitats (Fig. 10). Off-ridge juveniles expressed significantly smaller gapes, longer closing durations, slower angular velocities, and greater percent muscle contractions required to close the lower jaw compared to on-ridge juveniles for both muscles (Fig. 11).

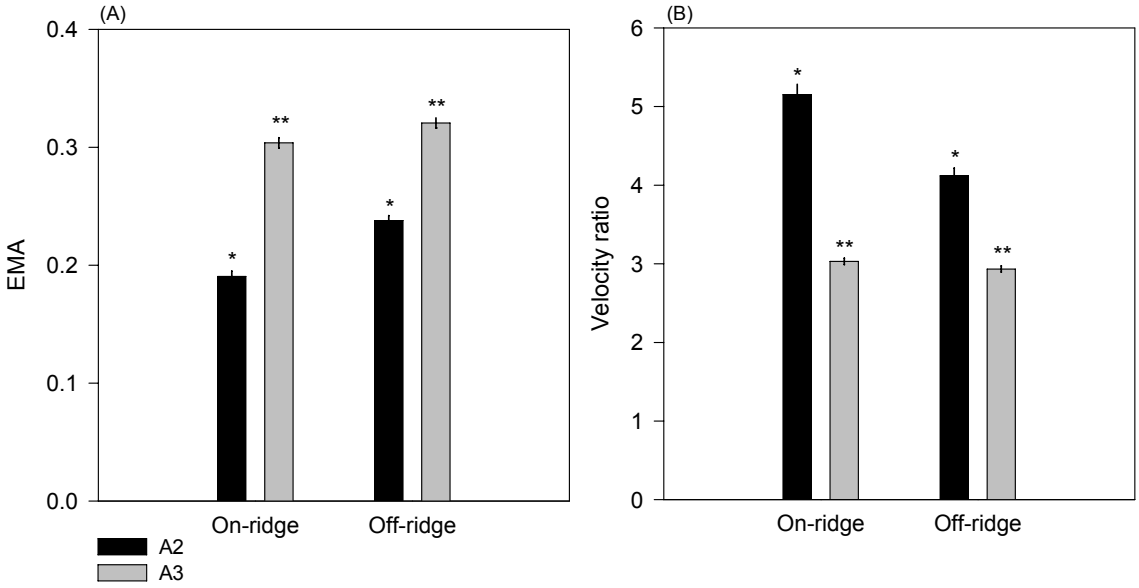

Figure 9. Mean (± S.E.M.) simulation results from the lever model. (A) effective mechanical advantage and (B) velocity ratio for the A2 and A3 muscles of juvenile red snapper from two different habitats.
* A2 muscle $p < 0.01$
** A3 muscle $p < 0.01$

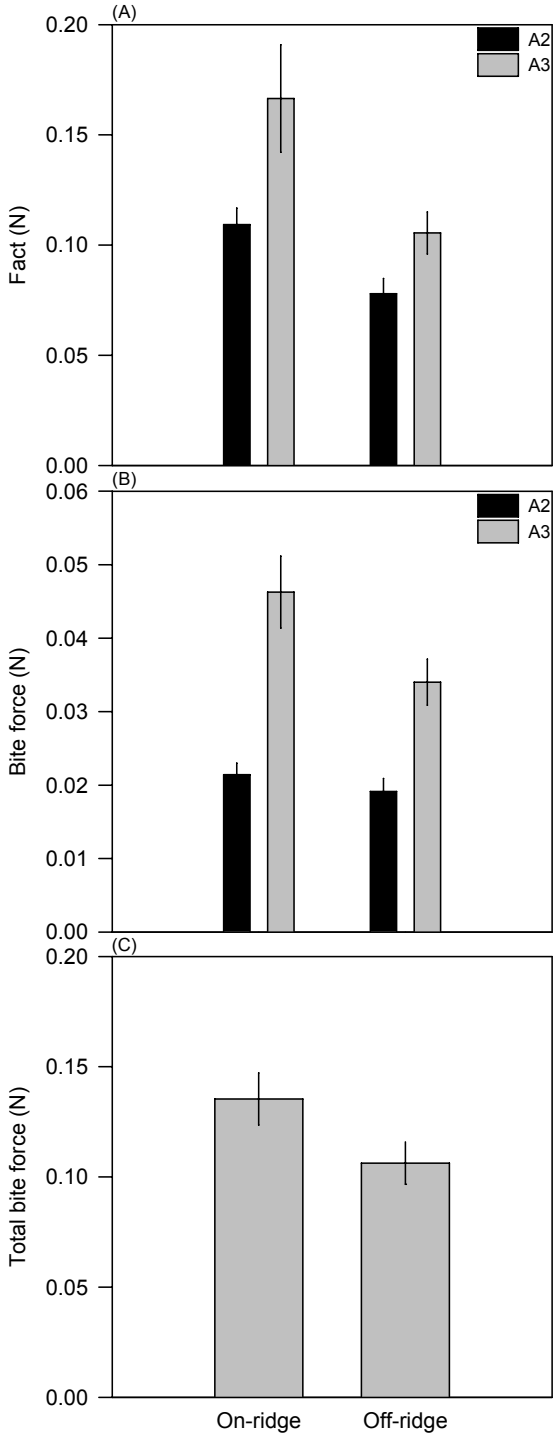

Figure 10. Mean (± S.E.M.) simulation results of lower jaw closing from the lever model for juvenile red snapper from two different habitats. (A) Muscle force exerted (Fact), (B) bite force contribution (Bite F) of the A2 and A3 muscles, and (C) total bite force.
* A2 muscle $p < 0.05$ (A,B), total bite force $p < 0.05$ (C)
** A3 muscle $p < 0.05$ (A,B)

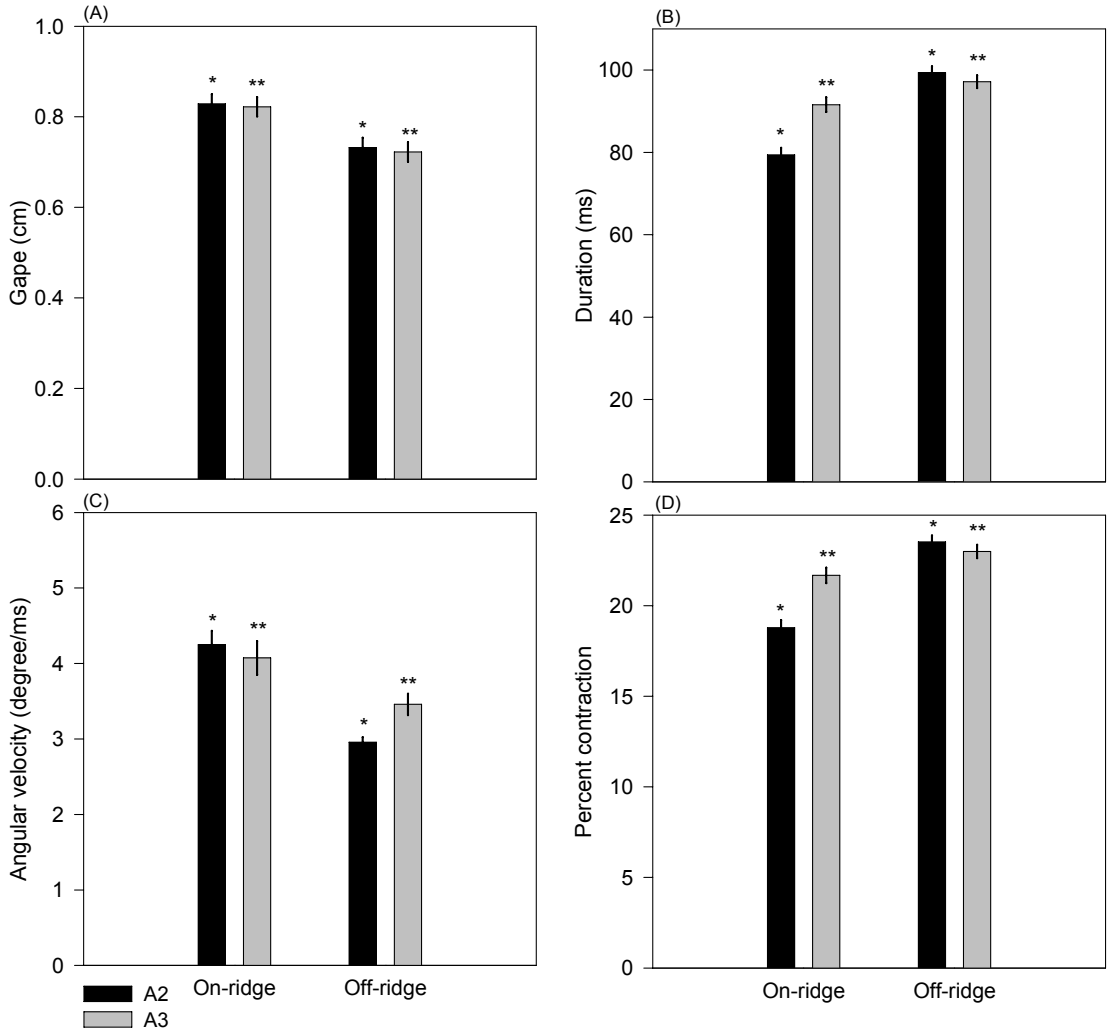

Figure 11. Mean (± S.E.M.) simulation results of lower jaw closing from the lever model for juvenile red snapper from two different habitats. (A) Gape change, (B) duration of lower jaw closing, (C) angular velocity of the lower jaw, and (D) percent contraction required to close the lower jaw.
* A2 muscle $p < 0.05$
** A3 muscle $p < 0.01$

Presumable function of the A2 and A3 muscles differed between habitats. The difference in velocity ratio of the A2 and A3 muscles in on-ridge juveniles was greater than in off-ridge juveniles (Fig. 9A). The closing duration and percent muscle contraction of the A2 muscle was shorter in on-ridge juveniles and larger in off-ridge juveniles compared to the A3 muscle (Fig. 11A,D). The angular velocity of the A2 muscle was greater than the A3 muscle in on-ridge juveniles and smaller than the A3 muscle in off-ridge juveniles (Fig. 11C). From these results the A2 muscle appears to be the dominant muscle in on-ridge juveniles for fast closing, whereas the A3 muscle appears to be the dominant muscle for fast closing in off-ridge juveniles.

General Muscle Action

To eliminate the effect of size and habitat variation, adult (n = 3) red snapper were modeled. These results from adults were only used to make general qualitative comparisons of the potential dynamic actions of the A2 and A3 muscles during lower jaw closing. They were not used for any statistical comparisons.

Overall, the A3 muscle was larger than the A2 in adults, both in length and cross-sectional area (Table 3). The A3 muscle contributed more force to overall bite force, had higher effective mechanical advantage, and thus a lower velocity ratio than the A2 muscle (Table 3). To accurately meet the functional demands of an actual feeding strike, the model dynamically calculated a high velocity at the start of jaw closure for prey capture and velocity was traded-off for high force

Table 3. Results of A2 and A3 muscle parameters from lever model simulations of lower jaw closing for adult red snapper.

	A2	A3
Muscle Length (cm)	4.19	7.60
CSA (cm2)	0.34	0.44
Fact (N)	5.42	6.96
Bite Force (N)	1.54	2.37
EMA	0.29	0.34
VR	3.02	2.70
Duration (ms)	110.5	95.7
Gape (cm)	4.60	4.56
Angular Velocity (degrees/ms)	2.71	3.44
% Contraction	26.2	22.6

as the lower jaw closed for biting (Fig. 12&14). Effective mechanical advantage also increased as the lower jaw closed because the muscle insertion angles were increasing relative to the length of the dentary (Fig. 13). Total duration of the A3 muscle in lower jaw closing was shorter than the A2 muscle (Table 3, Fig. 14). Since both muscles rotated through the same gape, the angular velocity of the A3 muscle was higher and the percent muscle contraction required to close the lower jaw was smaller than the A2 muscle (Table 3, Fig. 14). The trends observed in large juvenile A2 and A3 muscle function are in accord with data from adult model simulations, suggesting that when juveniles reach approximately 6 cm in length they switch to their adult feeding mechanism.

Validating the Model

Comparing model output to kinematic results tested the predictive accuracy of the jaw lever model. Least-squares regressions results for all juveniles are presented in table 4. To illustrate the trend in the model validation only data from a representative individual are presented in plots of lower jaw rotation (input variable) against gape displacement and gape angle velocity (output variables) in figure 15.

Gape Displacement

The lever model accurately predicted gape displacement in juvenile red snapper (Fig. 15A). When all feeding trials were pooled from both habitats ANCOVA results (Table 5) indicated no significant difference in slope between

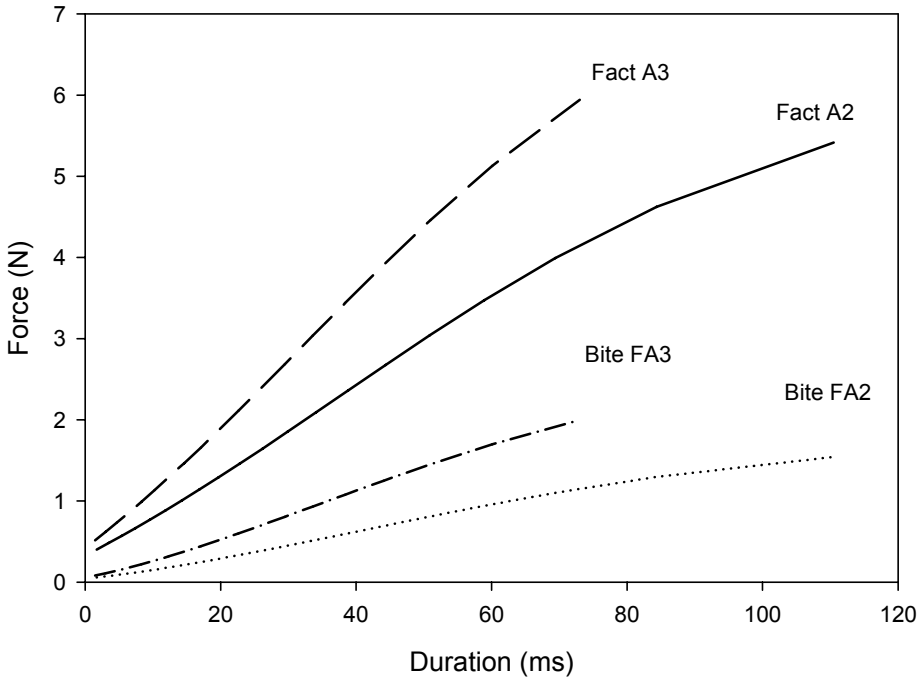

Figure 12. Muscle force exerted (Fact) and bite force contribution (Bite F) of the A2 and A3 muscles during model simulation of lower jaw closure of adult red snapper.

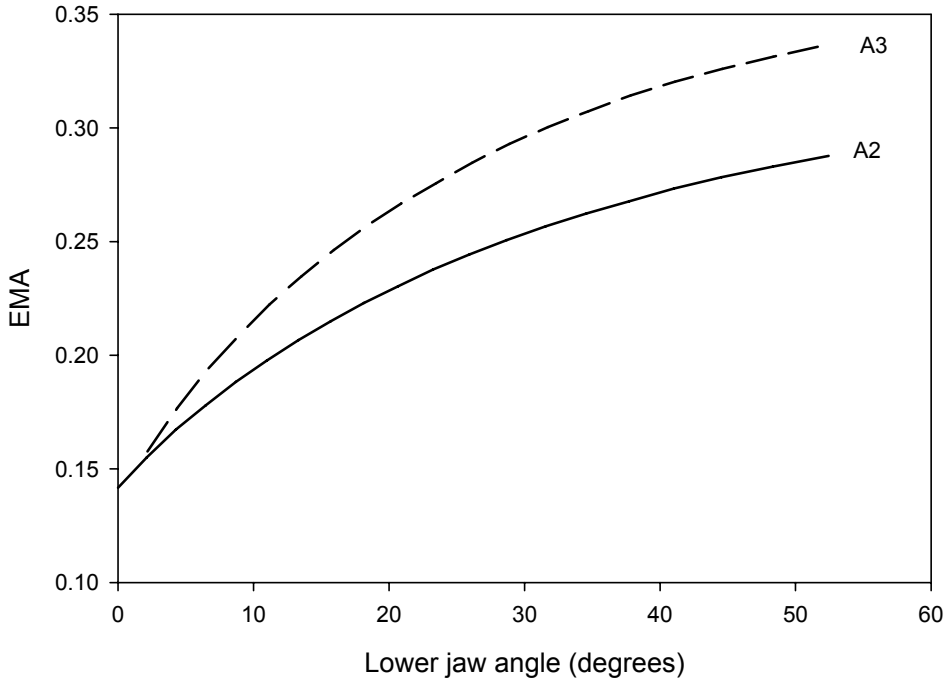

Figure 13. Effective mechanical advantage of the A2 and A3 muscles during model simulation of lower jaw closure of adult red snapper.

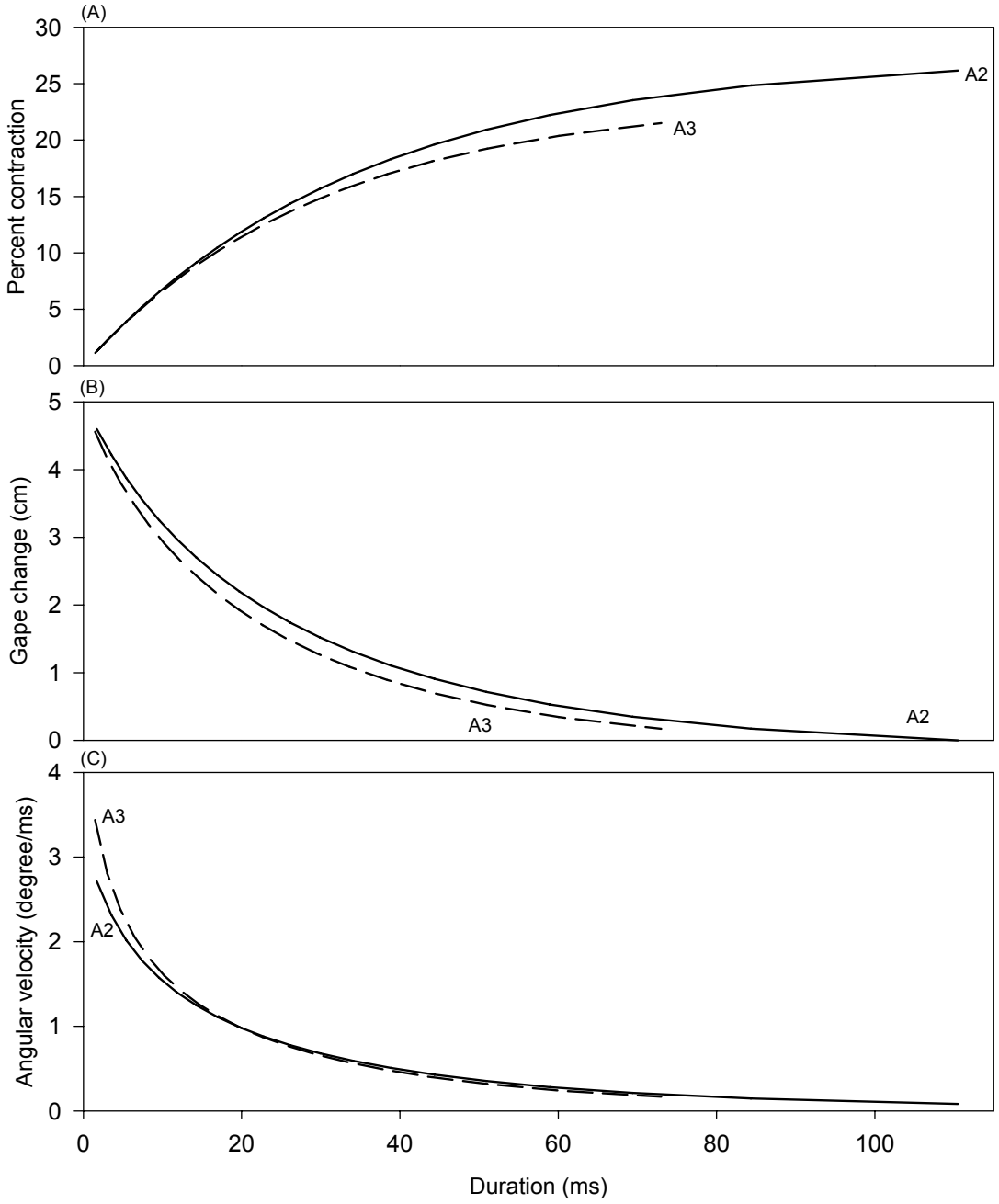

Figure 14. (A) Percent muscle contraction, (B) gape change, and (C) angular velocity of the A2 and A3 muscles during model simulation of lower jaw closure of adult red snapper.

kinematic and model data. However, the percent error of the model was greater than 25% (Table 5). As a result, habitats were separated to determine if the model was a better predictor for one habitat over the other. The model predicted gape displacement better in on-ridge juveniles (Table 5). ANCOVA results (Table 5) indicated no significant difference in slope between kinematic and model data. The slopes were exactly the same so the calculated percent error of the model was 0% (Table 5).

Gape Angle Velocity

The lever model also accurately predicted gape angle velocity in juvenile red snapper (Fig. 15B). All feeding trials from both habitats were pooled and ANCOVA results (Table 5) indicated no significant difference in slope between model and kinematic data. The percent error of the model was approximately 22% (Table 5). To examine if the model more accurately predicted one habitat over the other, habitats were separated. The model more accurately predicted gape angle velocity in off-ridge juveniles (Table 5). ANCOVA results (Table 5) indicated no significant difference in slope between kinematic and model data, and the percent error of the model was less than 13% (Table 5).

Feeding Performance

Feeding Phases

In general, a single prey capture event in juvenile red snapper was comprised of four phases: preparatory, expansive, compressive, and recovery.

Table 4. Least-squares regression equations from video kinematic and lever model predictions for juvenile red snapper. Video kinematics are divided, including all juveniles, only on-ridge juveniles, only off-ridge juveniles, and a representative individual expressing maximum jaw movements. Lower jaw rotation was used as the independent variable for all regressions.

	Lower jaw rotation x gape distance		Lower jaw rotation x gape velocity	
Video				
All fish	y = 0.154 + 0.011 x	adj. *R*2 = 0.77	y = 0.006 + 0.079 x	adj. *R*2 = 0.62
On-ridge	y = 0.134 + 0.015 x	adj. *R*2 = 0.77	y = -0.08 + 0.078 x	adj. *R*2 = 0.90
Off-ridge	y = 0.109 + 0.011 x	adj. *R*2 = 0.50	y = -0.068 + 0.071 x	adj. *R*2 = 0.94
Maximum individual	y = 0.048 + 0.014 x	adj. *R*2 = 0.92	y = 4.793 + 0.076 x	adj. *R*2 = 1.0
Model	y = -0.008 + 0.015 x	adj. *R*2 = 1.0	y = -0.169 + 0.062 x	adj. *R*2 = 0.94

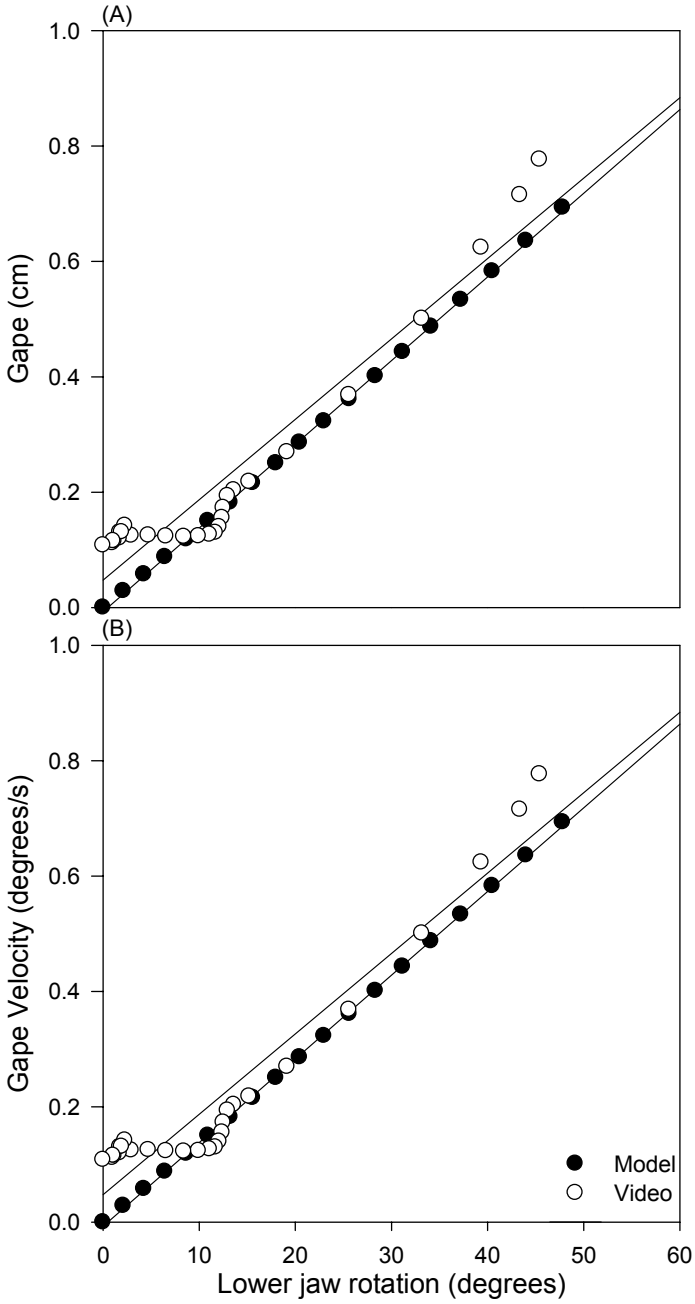

Figure 15. Regression lines comparing predictions of (A) gape change and (B) gape velocity from the lever model with video results from a representative juvenile red snapper.

Table 5. ANCOVA results testing differences between video kinematics and model predictions for juvenile red snapper. Slope and y-intercept entries are *p*-values. Lower jaw rotation was the independent variable for all tests. Significant differences indicate that the model fails to accurately predict the pair of variables. Percent error between the slope of model predictions and video kinematics is also listed. Results for variables are divided, including all fish, only on-ridge juveniles, only off-ridge juveniles, and a representative individual expressing maximum jaw movements.

	Slope	Y-intercept	Error (%)
Lower jaw rotation x gape distance			
All fish	0.14	0.00*	26.5
On-ridge	0.90	0.00*	0.00
Off-ridge	0.01	----	26.8
Maximum individual	0.48	0.00*	5.88
Lower jaw rotation x gape velocity			
All fish	0.06	0.00*	21.5
On-ridge	0.10	0.01	20.4
Off-ridge	0.18	0.01*	12.8
Maximum individual	0.20	0.00*	18.6

* $p < 0.01$

The preparatory phase began when the juvenile approached the prey with an open gape and the jaws initially moved, decreasing gape. The expansive phase began when gape began to increase until maximum gape was achieved. Hyoid depression began after gape began to increase. The compressive phase began at maximum gape and continued until gape reached its minimum value. The recovery phase began once gape was at its minimum and continued until the hyoid had fully returned to its starting position.

Feeding events always included an expansive and compressive phase. However, only 51.9% included an observed preparatory phase, and 59.3% included an observed recovery phase. It is likely that these phases occurred off camera. Feeding events with two gape cycles were common (23% of all feeding trials). When this occurred, a single preparatory phase led to replicating expansive and compressive phases, and then a single recovery phase concluded the feeding event. In these instances, the first gape cycle had a significantly larger gape and time to maximum gape was significantly longer, as well as longer preparatory and expansive phase durations (Table 6). Durations of the compressive and recovery phases were significantly longer during the second gape cycle (Table 6).

Off-ridge juveniles displayed more feeding trials with two gape cycles (37%) compared to on-ridge juveniles (8.3%). Typically, off-ridge juveniles would approach prey closely, capture it with minimal jaw movement, and then hold

Table 6. Mean (± S.E.M.) values of maximum kinematic variables for feeding events from juvenile red snapper that expressed two gapes.

	1st Gape	2nd Gape	
Variable	Mean	Mean	*p*-value
Maximum gape (cm)†	0.49 (±0.05)	0.29 (±0.03)	0.029*
Time to maximum gape (ms)†	96.4 (±16.8)	67.1 (±22.2)	0.021*
Maximum gape angle (degrees)	55.0 (±4.08)	31.6 (±3.09)	0.000*
Time to maximum gape angle (ms)	121.0 (±13.8)	46.0 (±6.24)	0.006*
Preparatory phase time (ms)	43.3 (±10.1)‡	40.0 (±0.00)**	0.905
Expansive phase time (ms)	90.0 (±15.6)	47.0 (±7.47)	0.024*
Compressive phase time (ms)	93.0 (±16.8)	111.0 (±16.1)	0.449
Recovery phase time (ms)	28 (±0.00)**	76.7 (±41.4)‡	0.676

* $p < 0.05$, †n = 9, ‡n = 6, **n = 1, all others n = 12

prey between jaws before reopening their mouth to reposition prey back to the pharyngeal jaws. On-ridge juveniles would typically approach and engulf prey items from a distance using a single explosive jaw movement. This resulted in juveniles from each habitat expressing different kinematic profiles.

Kinematic Profiles

To illustrate the trend in feeding performance among on-ridge individuals, a representative feeding sequence from one on-ridge individual is presented in figure 16A. Figures 17A and 18A represent the kinematic profile of the individual in figure 16A. The juvenile approached prey with mouth closed. Lower jaw depression began slightly before gape began to increase (0-8 ms; Figs. 16A, 18A). Gape and lower jaw rotation both reached their maximums at about the same time (0-36 ms; Figs. 16A, 18A). Jaw protrusion and hyoid depression began after mouth opening and reached their maximums after maximum gape was achieved (16-44 ms; Figs. 16A, 17A). Maxillary rotation and cranial rotation began to increase at the beginning of the feeding event and reached their maximums after maximum gape was achieved (0-44 ms; Figs. 16A, 18A). The hyoid, jaw tips, cranium, and maxillary returned to their original positions (44-144 ms; Figs. 16A, 17A, 18A) after the mouth had closed (36-112 ms; Figs. 16A, 17A, 18A).

A representative feeding sequence from one off-ridge individual is presented in figure 16B, and figures 17B and 18B represent the individuals' kinematic

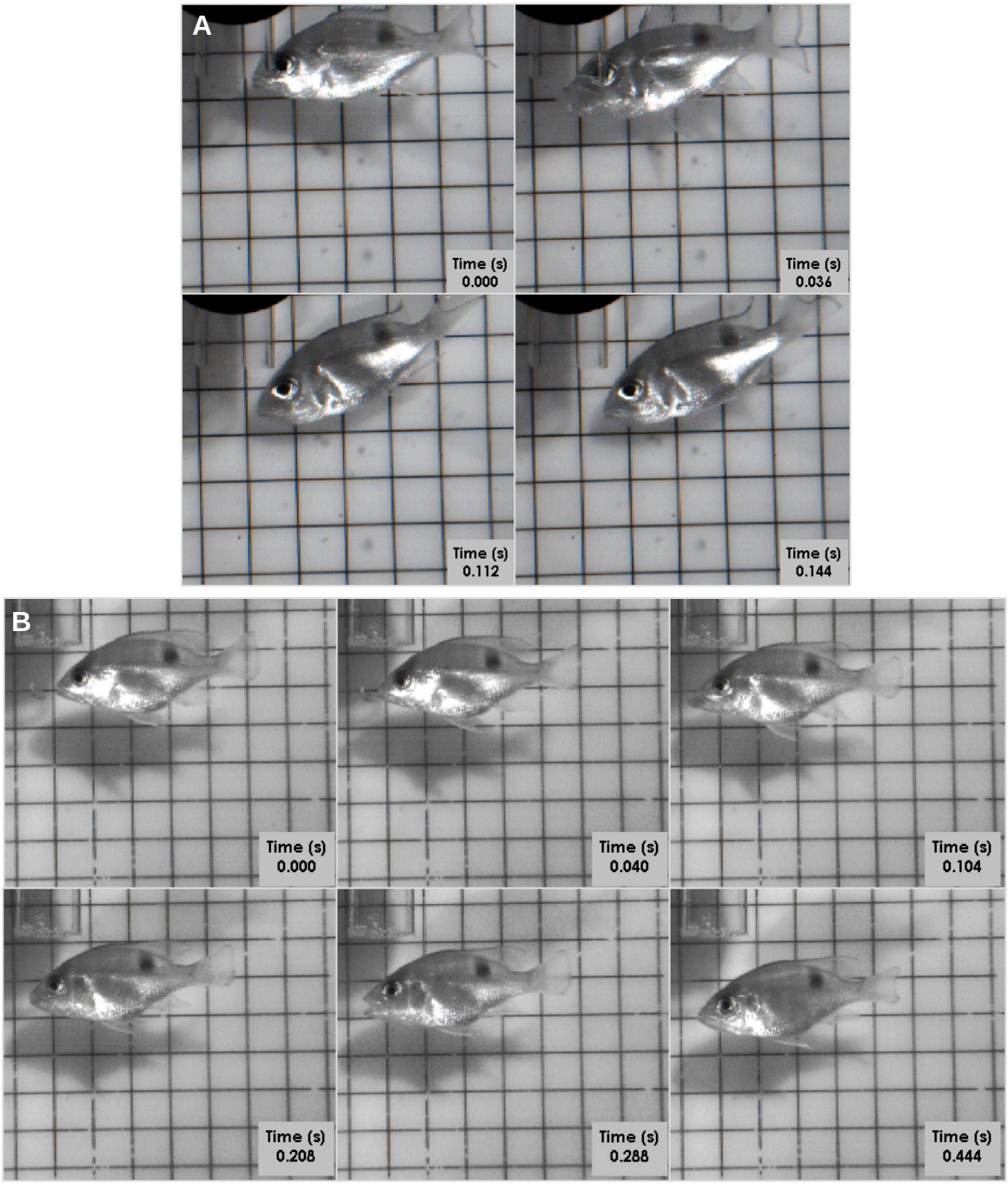

Figure 16. Selected high-speed video frames from a representative prey capture event for one individual juvenile red snapper from (A) on-ridge and (B) off-ridge.

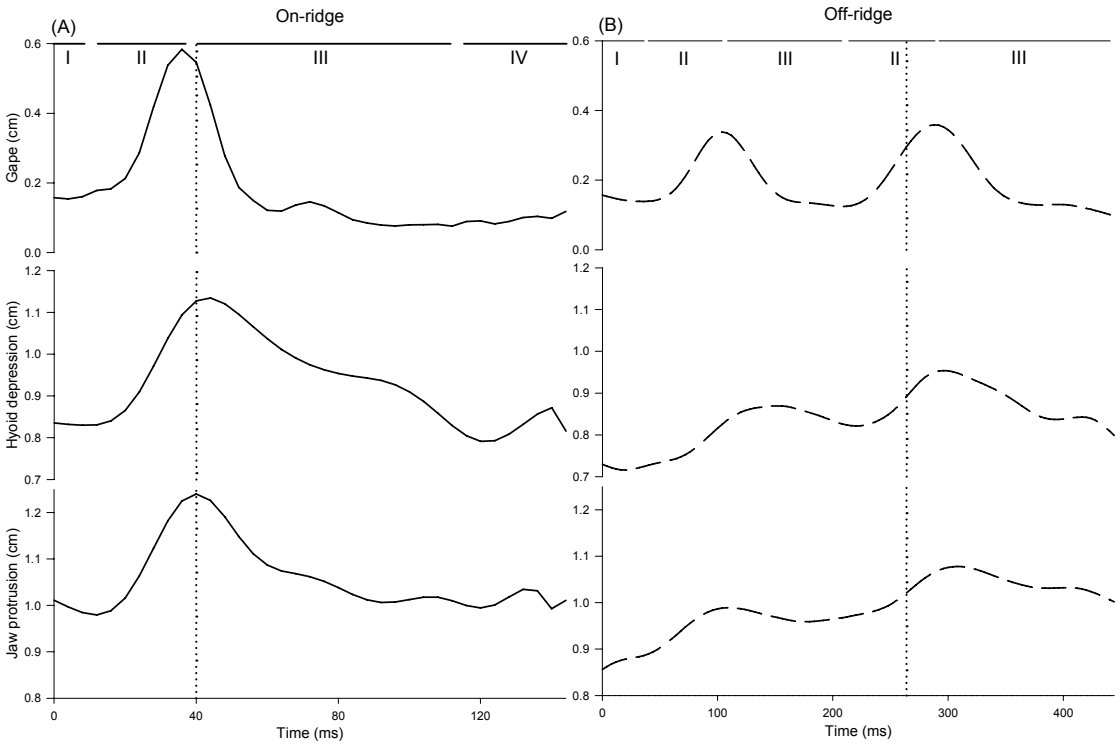

Figure 17. Kinematic profiles of displacement variables from a feeding event of a representative individual juvenile red snapper from (A) on-ridge and (B) off-ridge. Phases are shown by horizontal bars and labeled I-preparatory, II-expansive, III-compressive, and IV-recovery. Vertical lines represent time of prey capture.

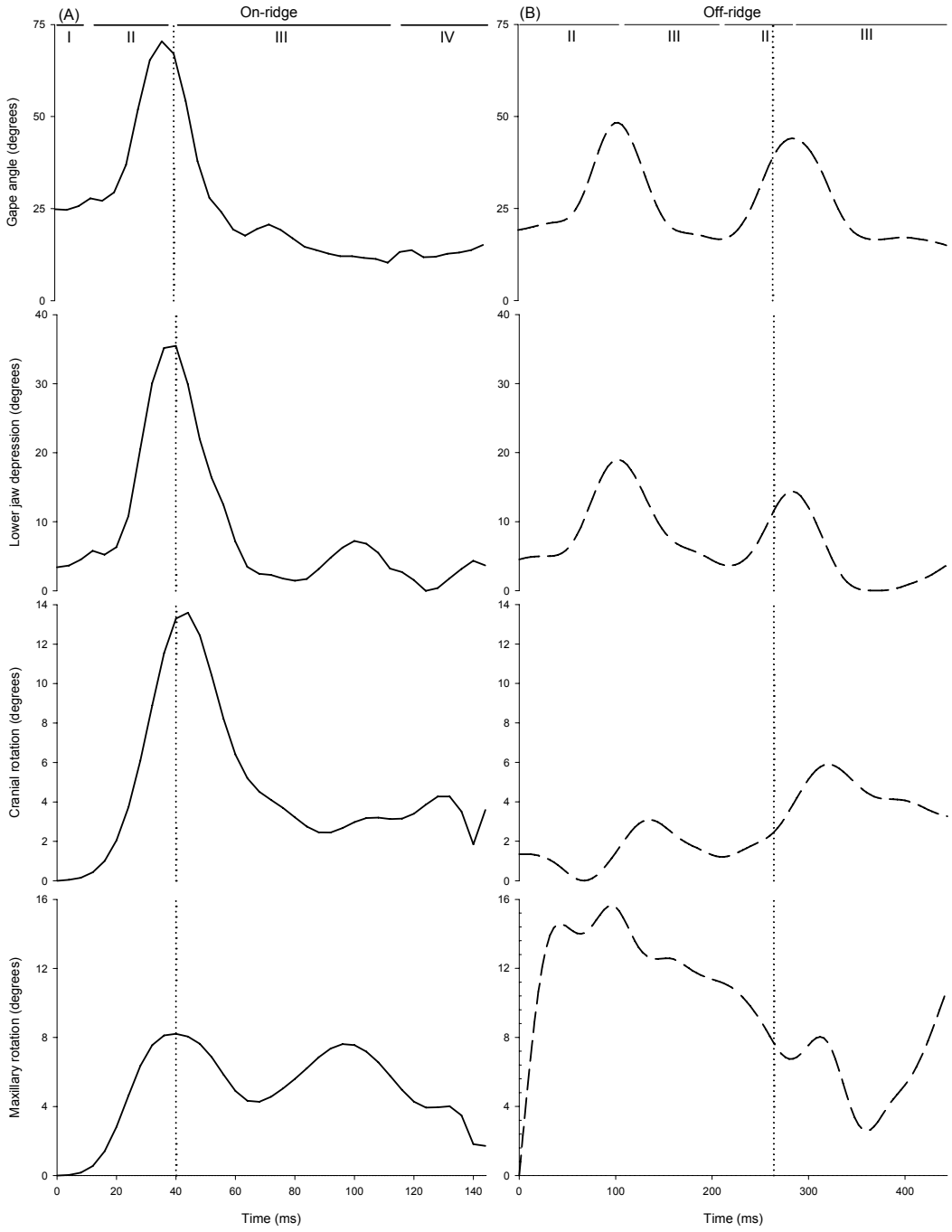

Figure 18. Kinematic profiles of angular variables from a feeding event of a representative individual juvenile red snapper from (A) on-ridge and (B) off-ridge. Phases are shown by horizontal bars and labeled I-preparatory, II-expansive, III-compressive, and IV-recovery. Vertical lines represent time of prey capture.

profile. Gape angle and lower jaw rotation began immediately and reached their maximums at the same time (0-104 ms; Figs. 16B, 17B). Gape displacement, however, initially decreased, delaying the starting time of gape displacement increase, but reached its maximum at the same time as gape angle and lower jaw rotation (44-104 ms; Figs. 16B, 17B, 18B). Since off-ridge juveniles generally captured the prey item and momentarily held it between the jaws, this resulted in a second gape cycle to move the prey to the pharyngeal jaws. During the second gape; gape angle, gape displacement, and lower jaw rotation all began and reached their maximums at the same time as each other (212-288 ms; Figs. 16B, 17B, 18B). Hyoid depression also initially decreased and began increasing approximately the same time as the first gape displacement and increased to its maximum, which occurred after the second gape maximum (44-296 ms; Figs. 16B, 17B). Jaw protrusion and maxillary rotation began to increase at the beginning of the feeding event and reached their maximums with the first maximum gape (0-104 ms; Figs. 16B, 17B, 18B). Jaw protrusion decreased and then increased again during the second gape, reaching a second maximum along with maximum hyoid depression (212-296 ms; Figs. 16B, 17B); maxillary rotation did not increase a second time. Cranial rotation increased slightly after the first gape displacement began and reached its maximum right after maximum hyoid depression (44-296 ms; Figs. 16B, 17B). After the second gape was achieved, the mouth closed and the hyoid, jaw tips, cranium, and

maxillary returned to their starting positions at the same time (284-444 ms; Figs. 16B, 17B, 18B).

Kinematic Variables

Table 7 displays the mean values for kinematic variables measured for the on-ridge and off-ridge habitats. Maximum displacement variables were significantly greater in on-ridge juveniles and time to these maximum displacement variables, although not significant, tended to be longer in on-ridge juveniles (Table 7, Fig. 19). Maximum angular variables and time to these maximum angle variables were greater in on-ridge juveniles, significantly for maximum cranial rotation and maximum maxillary rotation (Table 7, Fig. 20). Maximum angular velocities were faster in on-ridge juveniles for all angles, significantly for maximum lower jaw rotation velocity (Table 7, Fig. 21). Duration of the expansive, compressive, and recovery phases were all longer in on-ridge juveniles for a single gape cycle (using the gape cycle with maximum jaw displacement when there were two gape cycles); however, the preparatory phase was longer in off-ridge juveniles (Table 7, Fig. 22).

Time to Prey Capture

Prey capture time was shorter in on-ridge juveniles (Table 7). In on-ridge juveniles the time to prey capture occurred at approximately the time of maximum gape and significantly before the time of maximum hyoid depression and maximum jaw protrusion (Table 8, Fig. 17A). Time to prey capture also

Table 7. Mean (± S.E.M.) values for maximum kinematic variables for juvenile red snapper from two different habitats. *P*-values represent significant differences between habitats.

	On-ridge (n = 8)	Off-ridge (n = 9)	
Variable	Mean	Mean	*p*-value
Maximum gape (cm)	0.57 (±0.03)	0.43 (±0.02)	0.000*
Time to maximum gape (ms)	117.0 (±12.7)	98.9 (±8.85)	0.243
Maximum hyoid depression (cm)	1.18 (±0.02)	1.01 (±0.03)	0.000*
Time to maximum hyoid depression (ms)	152.2 (±17.7)	150.5 (±15.5)	0.942
Maximum jaw protrusion (cm)	1.28 (±0.02)	1.08 (±0.03)	0.000*
Time to maximum jaw protrusion (ms)	158.3 (±17.8)	150.9 (±15.6)	0.754
Maximum gape angle (degrees)	60.2 (±2.73)	54.2 (±8.12)	0.098
Time to maximum gape angle (ms)	116.5 (±12.8)	100.6 (±11.0)	0.289
Maximum lower jaw rotation (degrees)	173.0 (±1.95)	170.3 (±1.27)	0.259
Time to maximum lower jaw rotation (ms)	117.0 (±12.6)	110.3 (±16.0)	0.689
Maximum cranial rotation (degrees)	66.07 (±0.85)	63.61 (±0.71)	0.030*
Time to maximum cranial rotation (ms)	163.7 (±12.6)	145.3 (±11.7)	0.662
Maximum maxillary rotation (degrees)	103.9 (±1.04)	108.4 (±1.41)	0.015*
Time to maximum maxillary rotation (ms)	128.8 (±22.0)	123.3 (±0.01)	0.854
Maximum gape velocity (degrees/ms)	3.10 (±0.47)	2.11 (±0.39)	0.100
Maximum lower jaw rotation velocity (degrees/ms)	1.65 (±13.88)	0.98 (±0.16)	0.024*
Maximum cranial rotation velocity (degrees/ms)	0.41 (±0.08)	0.20 (±0.03)	0.132
Maximum maxillary rotation velocity (degrees/ms)	0.70 (±0.15)	0.58 (±0.12)	0.959
Preparatory phase time (ms)	19.0 (±4.83)	30.0 (±5.91)	0.171
Expansive phase time (ms)	107.0 (±12.3)	80.7 (±7.94)	0.073
Compressive phase time (ms)	141.7(±24.7)	103.9 (±11.8)	0.159
Recovery phase time (ms)	98.1 (±27.5)	55.0 (±12.5)	0.468
Time to prey capture (ms)	117.0 (±11.8)	124.0 (±12.6)	0.735

* $p < 0.05$

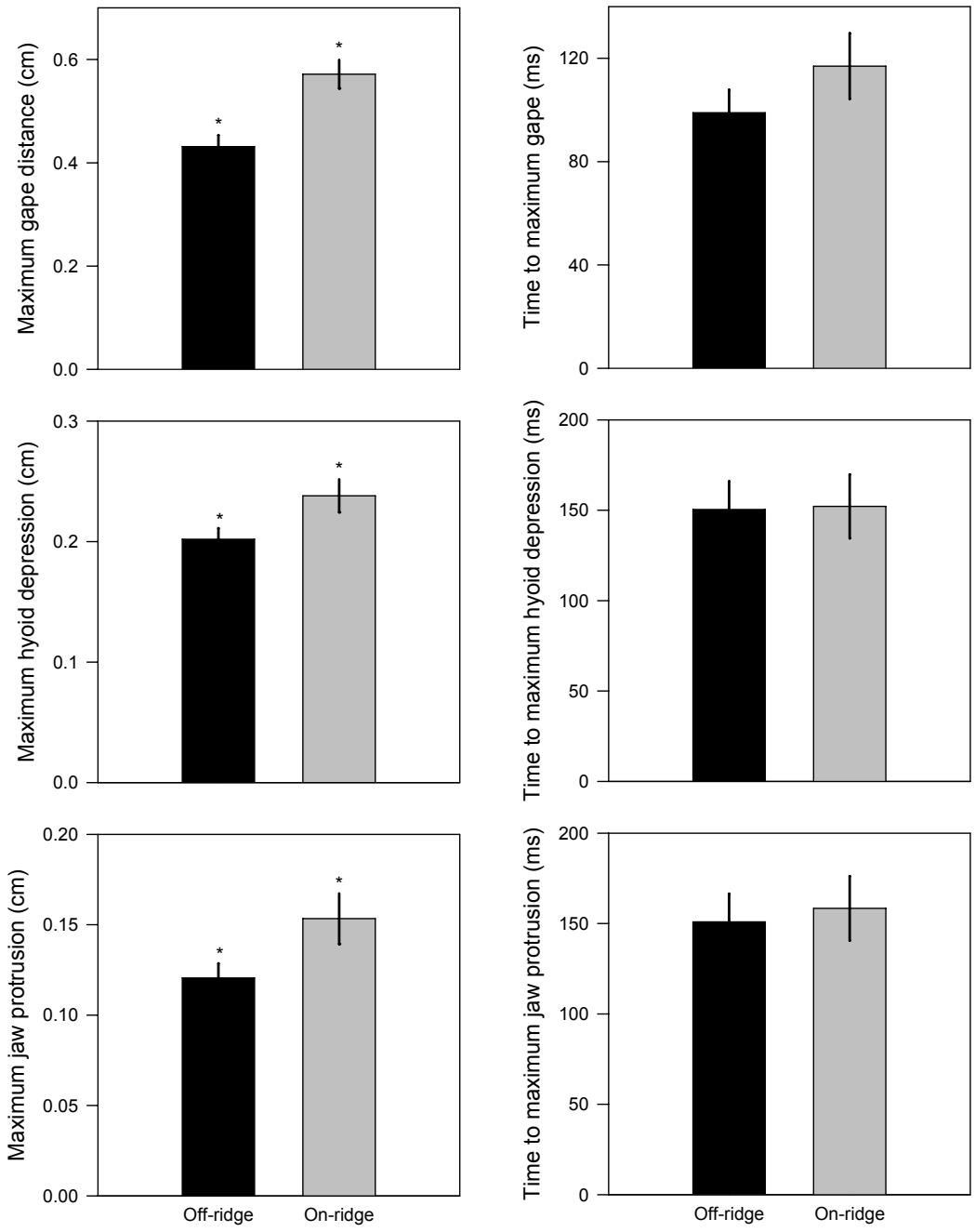

Figure 19. Mean (± S.E.M.) values of displacement variables measured during prey capture events of juvenile red snapper from on-ridge and off-ridge habitats. Significant differences between habitats are indicated by an asterisk, $p < 0.05$.

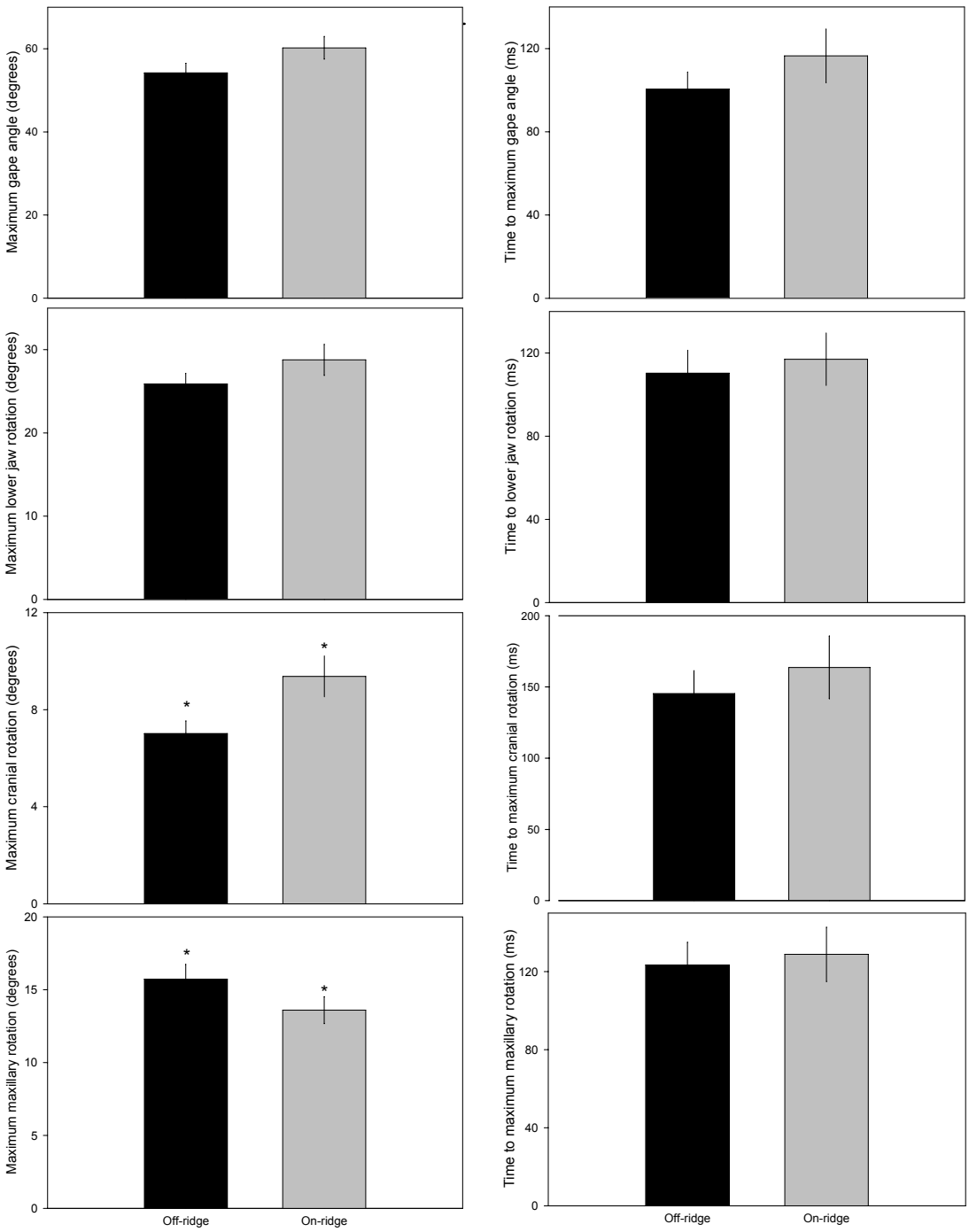

Figure 20. Mean (± S.E.M.) values of angular variables measured during prey capture events of juvenile red snapper from on-ridge and off-ridge habitats. Significant differences between habitats are indicated by an asterisk, $p < 0.05$.

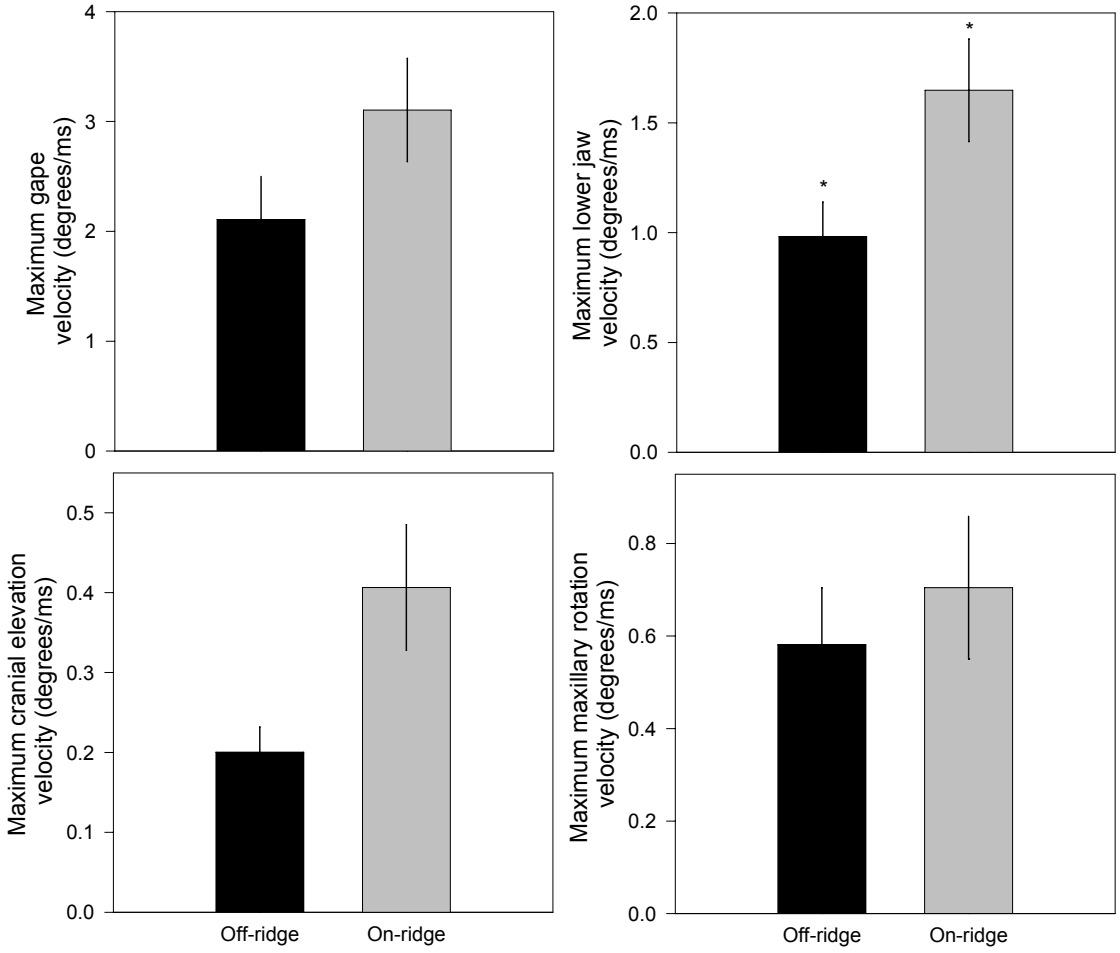

Figure 21. Mean (± S.E.M.) values of velocity variables measured during prey capture events of juvenile red snapper from on-ridge and off-ridge habitats. Significant differences between habitats are indicated by an asterisk, $p < 0.05$.

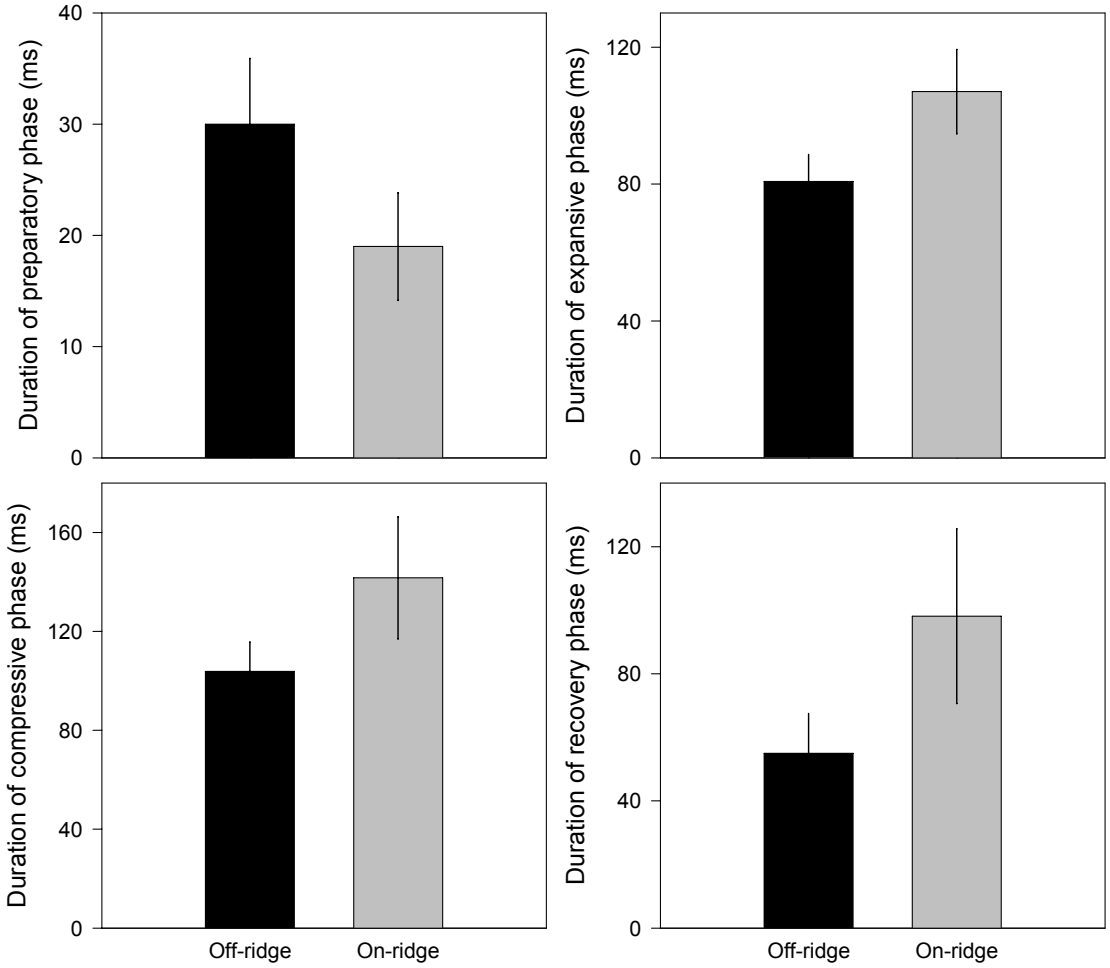

Figure 22. Mean (± S.E.M.) values of phase timings measured during prey capture events of juvenile red snapper from on-ridge and off-ridge habitats. There were no significant differences between habitats, $p > 0.05$.

Table 8. Mean differences between time to prey capture and kinematic timing variables for juvenile red snapper from two different habitats. Positive signs indicate that time to prey capture was longer, negative signs indicate that the kinematic variable time was longer. *P*-values represent significant differences between time to prey capture and kinematic timing variables.

Variable (ms)	On-ridge		Off-ridge	
	Mean difference	*p*-value	Mean difference	*p*-value
Time to maximum gape	0.00	0.65	0.04	0.02*
Time to maximum hyoid depression	-0.04	0.00*	-0.03	0.02*
Time to maximum jaw protrusion	-0.05	0.00*	-0.03	0.02*
Time to maximum gape angle	0.00	0.49	0.03	0.02*
Time to maximum lower jaw rotation	0.00	0.72	0.02	0.19
Time to maximum cranial elevation	-0.05	0.00*	-0.03	0.03*
Time to maximum maxillary rotation	-0.01	0.22	-0.00	0.91

* $p < 0.05$

occurred at approximately the time of maximum gape angle and maximum lower jaw depression, significantly before the time of maximum cranial rotation, and before the time of maximum maxillary rotation (Table 8, Fig. 18A). In off-ridge juveniles time to prey capture occurred significantly after the time of maximum gape and before the time of maximum hyoid depression and maximum jaw protrusion (Table 8, Fig. 17B). Time to prey capture also occurred significantly after the time of maximum gape angle, after the time of maximum lower jaw rotation, significantly before the time of maximum cranial rotation, and before the time of maximum maxillary rotation (Table 8, Fig. 18B).

Phenotypic Variation

Shape analysis further supports morphological and behavioral differences in juvenile red snapper between habitats. Lateral body morphology of juvenile red snapper significantly differed between the two habitats ($p < 0.01$) and also differed across size ($p < 0.01$). Habitat effect accounted for 1.6% of the total morphological variation and size effect accounted for 9.1%. The effect of habitat was small in magnitude, but high in significance. Thin plate spline transformation grids illustrate changes along the shape axis (Fig. 23) and habitat and size canonical scores are presented in Table 9. The habitat effect axis indicated that off-ridge juveniles had a deeper head and body than on-ridge juveniles (Table 9, Fig. 23). The size effect axis indicated that as juvenile body size increased the head and body became deeper.

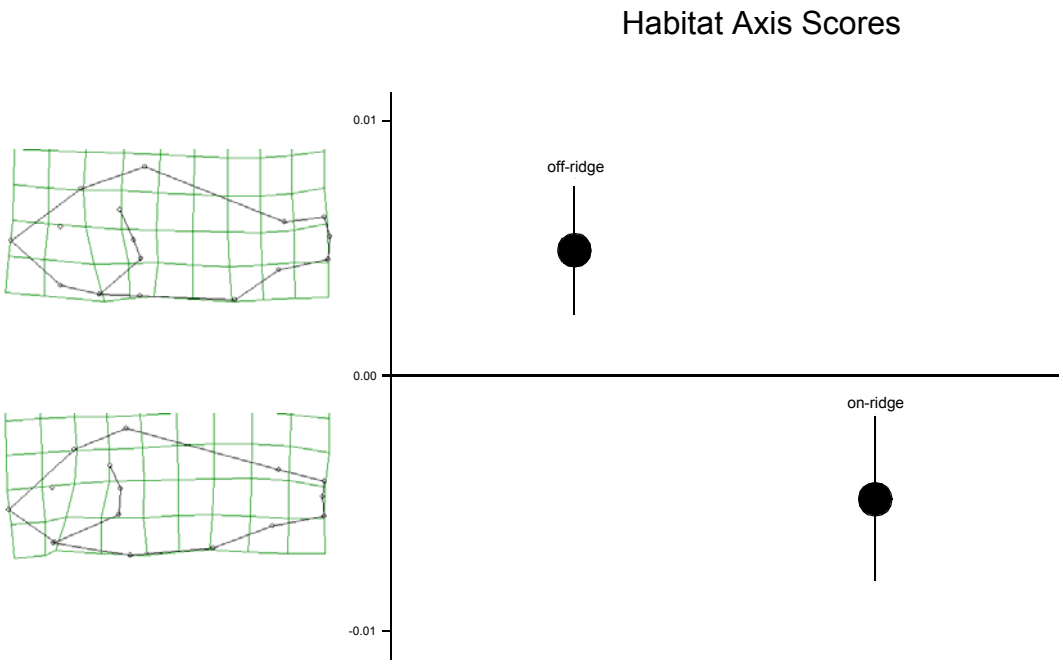

Figure 23. Morphological responses by juvenile red snapper to habitat. Habitat axis scores plotted with transformation grids for illustration. Grids are magnified 10x to enhance habitat effect.

Table 9. Pearson correlations between superimposed lateral landmark coordinates from juvenile red snapper and the habitat and size canonical score. Correlations ≥0.5 are in bold to emphasis landmarks that vary the most among juveniles from the two habitats or from the three size classes. Positive signs indicate increases in x or y coordinates associated with habitat and size; negative signs indicate the opposite relationship. Landmarks are identified in Fig. 5.

Habitat axis score	Allometry score	Landmark
-0.51	**-0.67**	X2'
0.25	-0.39	Y2'
-0.30	0.11	X4'
0.46	0.49	Y4'
-0.33	**-0.51**	X6'
0.36	0.45	Y6'
0.24	0.33	X7'
0.37	**0.54**	Y7'
-0.06	-0.04	X8'
-0.19	0.04	Y8'
-0.59	**-0.53**	X9'
0.41	0.02	Y9'
-0.32	**-0.55**	X10'
0.15	-0.29	Y10'
-0.22	**-0.63**	X11'
-0.02	**-0.51**	Y11'
-0.07	-0.22	X12'
-0.42	-0.10	Y12'
0.31	**0.62**	X13'
-0.57	-0.16	Y13'
0.01	**0.62**	X14'
-0.11	0.04	Y14'
0.60	-0.14	X15'
-0.54	-0.32	Y15'
0.05	-0.16	X16'
-0.26	**-0.58**	Y16'
0.26	0.37	X17'
-0.01	0.30	Y17'
0.13	**0.52**	X18'
-0.12	0.27	Y18'
0.19	0.39	X19'
0.05	0.13	Y19'

Stomach Content Analysis

Prey items were divided into the following categories, including empty stomachs: copepods (most likely *Corycaeus amazonicus*), mysids (Order Mysidacea), shrimp (Family Penaeidae), crab (Order Decapoda, possibly mole crabs), fish (InfraClass Teleostei, a single *Saurida brasilensis* was identified), and unidentified items. Stomach contents were extremely digested and as a result much of the contents could not be identified and the items that remained were difficult to classify. Also, because of advanced digestion, the weight of individual prey items could not be made for the majority of the stomach contents. Therefore, a qualitative assessment of stomach contents was made based on the presence of prey items from each category.

Ontogeny

Percent frequency of occurrence of prey items found in juvenile red snapper stomachs for each size class is represented in figure 24A. Copepods were present in more that 20% of stomachs from small and medium juveniles, none were present in large juveniles. Mysids were rare, present in less that 2% of stomachs from small juveniles and less than 5% from medium juveniles. Shrimp were the most abundant prey type for all size classes, present in more than 30% of small and medium juvenile stomachs and in more than 50% of large juvenile stomachs. It was also qualitatively observed that as juveniles increased in size so did individual shrimp size found in the stomachs. Crabs were found in less than 2% of small juvenile stomachs, approximately 10% of medium juvenile

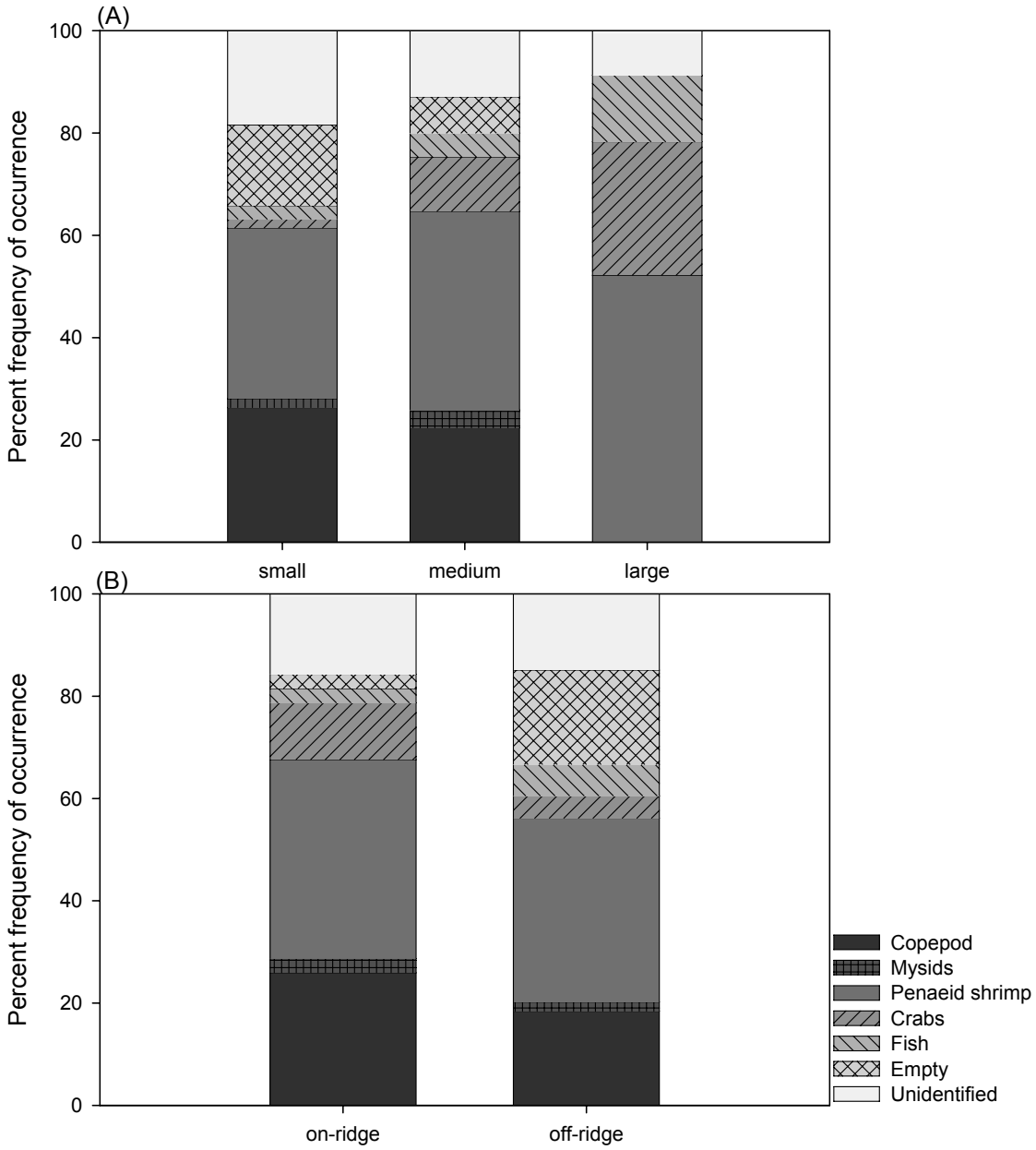

Figure 24. Percent frequency of occurrence of prey items in juvenile red snapper stomachs from (A) three size classes and (B) two habitats.

stomachs, and more than 20% of large juvenile stomachs. Fish were found in less than 5% of small and medium juvenile stomachs and in 13% of large juvenile stomachs. Approximately 16% of small juvenile stomachs and approximately 7% of medium juvenile stomachs were empty. No large juvenile stomachs were empty. Unidentified items were present in more than 18% of small juvenile stomachs, approximately 13% of medium juvenile stomachs, and approximately 9% of large juvenile stomachs.

Habitat

Habitat effect on stomach content was also examined. Percent composition of prey items found in juvenile red snapper stomachs from the two habitats is represented in figure 24B. Copepods were slightly more abundant in on-ridge juvenile stomachs (approximately 20%) than in off-ridge juvenile stomachs (approximately 18%). Mysids were rare, present in approximately 2% of stomachs from juveniles from both habitats. Shrimps were more abundant in off-ridge juvenile stomachs (36%) than in on-ridge juvenile stomachs (approximately 30%). Crabs were more abundant in on-ridge juvenile stomachs (approximately 9%) than in off-ridge juvenile stomachs (approximately 4%). Fishes were more abundant in off-ridge juvenile stomachs (approximately 6%) than in on-ridge juvenile stomachs (approximately 2%). Off-ridge juveniles had more empty stomachs (18%) than on-ridge juveniles (2%). Juveniles from both habitats had approximately the same amount of unidentified content, 12% in on-ridge juveniles and 15% in off-ridge juveniles.

DISCUSSION AND CONCLUSIONS

This study provides new data on the development of juvenile red snapper during early life history stages. Juvenile red snapper undergo ontogenetic changes in their morphology, in both the feeding apparatus and body and head shape, and feeding behavior that are concurrent with a shift in prey resources. Juvenile red snapper remain in nursery habitats until approximately 7 cm in length then migrate to adult populations in deeper waters (Szedlmayer and Lee 2004). It has been demonstrated that diet change in juveniles initiates this movement between habitats for juvenile red snapper (Szedlmayer and Lee 2004) and in other species (*e.g.* Cocheret de la Morinière *et al.* 2003, Monteiro *et al.* 2005). At this transitional stage, juveniles of some fish species are large enough to reduce predation risks and have developed the ability to consume adult prey items (Ward-Campbell and Beamish 2005). This study supports these results and provides data regarding the mechanisms of this transition. In addition, juvenile red snapper from different habitats exhibited differences in their feeding mechanism, feeding behavior, as well as their head and body morphology, providing further information on how nursery habitat choice may affect recruitment of juveniles to the adult population.

Ontogenetic Effects

Ontogenetic shifts in diet by fishes can be associated with increased prey handling proficiency, acquisition of larger prey items, or a change in feeding

mode (Luczkovich *et al.* 1995, Wainwright and Richard 1995). Variations in feeding mode can result from changes in the feeding mechanism. Measurements of mechanical advantage based on jaw lever ratios have been used to describe the relationship between feeding mechanics and ecology of many fishes (e.g. Barel 1983, Westneat 1994, 2004, Wainwright and Richard 1995). Lever ratio data from this study demonstrated that there was an ontogenetic shift in the feeding apparatus of juvenile red snapper with lower jaw movement becoming slower and more forceful as juvenile size increased (Fig. 6). A large lever ratio (indicating greater force transmission) has been shown to successfully predict a hard prey diet and a small lever ratio (indicating increased velocity) has been shown to predict an elusive prey diet (Barel 1983, Westneat 1994, 2004, Wainwright and Richard 1995). The lever ratios from this study suggest that an ontogenetic shift in morphology occurs that enables large juveniles to exploit harder prey types, implying that there is a diet switch in juveniles from mainly elusive prey items to the inclusion of hard prey items when they reach 6 cm in length. This diet switch was observed in juvenile red snapper at 6 cm based on gut content data from this study (Fig. 24A) and previous studies (Bradley and Bryan 1976, Szedlmayer and Lee 2004). Further, evidence from shape analyses demonstrated that small juveniles were relatively more streamlined, whereas large juveniles exhibited deeper bodies and were less streamlined. These changes in body shape also suggest that as juveniles grow in size they transition away from an elusive diet and eventually attain the ability

to consume harder prey types (Svanbäck and Eklöv 2002, Hjelm *et al.* 2003). Adult red snapper in this study demonstrated a lower jaw movement that was slow and forceful (Table 3), which coincides with adult diet consisting of hard prey items, such as crabs (Bradley and Bryan 1976). Data from this study demonstrates that the morphological and biomechanical switch observed in juveniles is the initial modification towards the adult feeding mode.

Modeling data show that the potential function of the A2 and A3 adductor muscles changed ontogenetically for red snapper. In small juveniles, the A2 muscle dominated lower jaw movement, whereas the A3 dominated in large juveniles. As expected, cranial morphometric measurements increased with juvenile size. These increases resulted in an overall increase in force (Fig. 7), gape, and angular velocity (Fig. 8) for both muscles. Since angular velocity increased with size, lower jaw closing duration concomitantly decreased, as did the percent muscle contraction (due to an increase in mechanical advantage) required to close the jaw (Fig. 8) for both muscles. The A3 muscle increased in size at a faster rate than the A2 muscle, causing the A3 muscle morphology, and function, to change to a greater extent over ontogeny than the A2 muscle (Table 2). As the A3 inlever became longer, A3 force contribution increased (Fig. 7) due to an increase in mechanical advantage. As the A3 muscle became longer the angular velocity increased, resulting in shorter closing durations and less percent muscle contribution to close the lower jaw (Fig. 8), assuming the dominant role in lower jaw closing. The A3 muscle was the dominate muscle in

lower jaw closing in adult red snapper as well, again supporting data from this study that there is a transition to an adult feeding mechanism, from A2 muscle dominance to A3 muscle dominance, in juveniles at 6 cm.

Habitat Effects

The lower jaw lever model of juvenile red snapper from the two habitats illustrated significant differences in their potential feeding capabilities. The lower jaw lever model calculated lever ratios that were significantly greater in off-ridge juveniles, indicating that off-ridge juveniles had greater force transmission and on-ridge juveniles had greater jaw closing velocity (Fig. 9). These lever ratios predict that off-ridge juveniles have the ability to crush harder prey types, or bite off pieces of larger prey, whereas on-ridge juveniles have the ability to capture small, elusive prey. The lower jaw model also predicted faster angular velocities and shorter closing durations for on-ridge juveniles, which further supports suction feeding on small, elusive prey.

Results from feeding performance trials of juvenile red snapper further support differences in feeding capability predicted by the lower jaw model. Actual feeding events of juvenile red snapper demonstrated that on-ridge juveniles used suction feeding, which is supported by kinematic data. For example, on-ridge individuals exhibited greater displacement variables, larger angular variables (except for maxillary rotation), and greater angular velocities, compared to off-ridge juveniles, and these characteristics are typical of suction feeders (Liem 1980, van Leeuwen and Muller 1984, Svanbäck *et al.* 2002). Off-

ridge juveniles exhibited more biting behavior and utilized two gape cycles to manipulate prey items resulting in longer prey capture times.

Juvenile red snapper also exhibited phenotypic plasticity in response to differences between habitats. Shape analysis has been used previously to demonstrate the expression of phenotypic plasticity of an organism induced by varying environmental factors (Robinson and Wilson 1996, Robinson *et al*. 1996, Svanbäck and Eklöv 2002, 2003, Doughty and Reznick 2004, Parsons and Robinson in press). Some organisms have the ability to adapt to variable conditions, becoming polymorphic, in order to exploit the most abundant resources. For example, water column position and associated available prey can affect the morphology and shape of an individual allowing it to exploit a particular food resource, which increases its foraging efficiency (Lavin and McPhail 1986, Ehlinger and Wilson 1988, Malmquist 1992, and Parsons and Robinson in press), and affects the individuals' growth rate (Svanbäck and Eklöv 2003). Such studies reveal that streamlined bodies are associated with midwater feeders and are optimal for high velocity prey capture on elusive prey types. In contrast, deeper bodies are associated with low velocity and high maneuverability, and this is optimal for benthic foragers that feed on hard prey types (Ehlinger and Wilson 1988, Malmquist 1992, Motta *et al.* 1995, Robinson and Wilson 1996, Robinson *et al*. 1996, Hjelm *et al.* 2003, Svanbäck and Eklöv 2003). Other studies have manipulated prey items in controlled experiments and results revealed a morphological difference in head shape, streamlined

versus deep head shape, when fish were fed soft, elusive prey versus harder prey types, respectively (Meyer 1987, Wimberger 1991, 1992, Hegrenes 2001, Parsons and Robinson in press). In the present study, off-ridge juvenile red snapper had deeper heads, while on-ridge juveniles had more streamlined heads. Among the selected landmarks, the branchiostegal ray point (15) moved anteriorly in on-ridge juveniles (Table 9, Fig. 23). Previous studies show that this point moves in the same direction in fish fed soft prey items (T. DeWitt unpublished). Therefore, juvenile red snapper head and body shape differences suggest that the diet of the more streamlined shaped juveniles present in the on-ridge habitat consists of softer prey items, or perhaps smaller items that are ingested whole. Conversely, the diet of deeper bodied off-ridge juveniles consists of harder prey types, or pieces of larger prey.

Intraspecific polymorphism can be the result of genetic differences between individuals in a population and environmentally induced phenotypic plasticity. Juveniles used in kinematics and shape analyses were collected on the same day. Therefore equally sized individuals are presumably from the same cohort; differences between habitats should not be a result of genetic variation. Juveniles used in the jaw lever model were potentially from different cohorts, since they were collected on different dates. However, sampling from genetically different cohorts has been shown to not be the driving force behind polymorphic patterns (Olsson 2006). Additionally, phenotypic plasticity has been demonstrated to explain morphological variation more than genetic variation

(Robinson and Wilson 1996), therefore suggesting that morphological differences in juvenile red snapper are primarily due to habitat effects.

Morphological and performance differences of juvenile red snapper feeding from the two habitats were reflected in their actual diet. Stomach content data revealed that juveniles from both habitats consumed the same amount of mysids and penaeid shrimps. However, on-ridge juveniles appeared to consume more copepods and crabs, whereas off-ridge juveniles appeared to consume more fish. Qualitative observations of feeding events and stomach contents support our hypothesis that on-ridge juveniles used suction as their primary feeding mode and off-ridge juveniles used biting as their primary feeding mode. In captivity, off-ridge juveniles were observed actively biting the prey given to them, as well as each other. Off-ridge juveniles would approach other juveniles and bite them to remove large pieces of flesh, or completely bite them in half. The majority of fishes identified in off-ridge juvenile stomach contents were large pieces of fishes, not whole fishes. This is consistent with the behavior observed in captivity. On-ridge juveniles were observed using suction to capture prey given, and were rarely seen biting each other. The greater amount of copepods found in on-ridge juveniles suggests that they are efficient at targeting small, elusive prey items from the water column. The majority of crabs found in on-ridge juvenile stomachs were small in size and were swallowed whole. It is likely that on-ridge juveniles used their suction ability to remove crabs and other prey from burrows or crevices, whereas the crab prey found in off-ridge juvenile

stomachs were broken pieces of larger crabs, suggesting they were too large to swallow whole, and were crushed before consumption. This suggests that off-ridge juveniles have the morphological capability to crush hard prey and bite pieces of fishes more effectively than on-ridge juveniles, whereas on-ridge juveniles are limited by their morphology and target prey items that can be swallowed whole.

The realized niche of juvenile red snapper depends on the interactions of their phenotypic characteristics, governing their feeding capabilities, and their environment, such as available prey. Therefore, not only having the feeding capability but also the opportunity is important in determining feeding patterns. Differences between on-ridge and off-ridge habitats most likely result in variations in prey availability. Juvenile red snapper are opportunistic feeders that exhibit flexibility in their feeding habits (Szedlmayer and Lee 2004) allowing them to exploit the most available resources found on either habitat. Targeting different prey may initiate the development of different feeding mechanisms between habitats, and could further result in changes in the timing of developmental events (Meyer 1987).

In this study, it is likely that ontogenetic modifications in feeding ability resulted in size-related diet shifts. Habitat influenced the transition between these ontogenetic stages, resulting in off-ridge juveniles possessing the ability to consume fish earlier than on-ridge juveniles at the same body size. A fish diet is high in caloric value, so an earlier switch to piscivory promotes fast growth and

survival (Persson and Brönmark 2002, Post 2003, Graeb *et al*. 2005), which may explain the higher growth rates reported in off-ridge areas. In general, faster growing fish, due to an early switch to piscivory, represent the population majority within the cohort, and therefore contribute more recruiting individuals to the adult population (Olson 1996, Ludsin and DeVries 1997, Persson and Brönmark 2002). Based on the definition of a nursery by Beck *et al*. (2001), higher growth rates and higher recruitment success may indicate that the off-ridge habitat represents better nursery habitat than on-ridge areas for juvenile red snapper.

This study provides additional data that supports the importance of off-ridge habitats to the recruitment success of juvenile red snapper. Elimination or destruction of off-ridge habitat, due to events such as trawling or development of coastal artificial reef systems on mud habitats, may negatively impact the red snapper fishery by limiting the recruitment success of juveniles to the adult population. Therefore, it is important that off-ridge areas be included in the management of essential nursery grounds for juvenile red snapper.

Juveniles ranging from 1.8-10.8 cm SL were targeted in this study, but the inclusion of more ontogenetic stages from larvae to adults would provide greater resolution in red snapper feeding modifications across their entire life history. Conducting a bioenergetics study on juveniles from Freeport Rocks Bank, as well as juveniles from different banks where higher growth rates were present on-ridge would provide a more thorough understanding of the differences in

growth rates between habitats. In addition, an investigation of the feeding mechanisms of hatchery raised red snapper would also be important in understanding their capability to modulate feeding behavior, their ability to adapt to new habitats, and to ensure that captive reared red snapper undergo the morphological and feeding performance shift observed in wild red snapper.

In summary, the feeding apparatus of juvenile red snapper enables exploitation of prey resources located in their nursery habitat. Juveniles can begin utilizing new resources as they grow and their morphology and feeding performances shift. Over ontogeny, juveniles develop the morphological capability to consume harder prey types that are more typical of adult diets, and can therefore effectively move into the adult population. Off-ridge juveniles have the morphological capability to consume hard prey types, but more importantly fish. This earlier switch to piscivory may increase the growth rates of off-ridge juveniles, increasing off-ridge juvenile survival and recruitment to adult populations. Therefore, off-ridge areas may serve as essential nursery habitat of red snapper and should be protected.

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